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of the 3rd
CONE AND SEED INSECTS
WORKING PARTY
CONFERENCE

Working Party S2.07-01

June 26 - 30, 1988
Victoria, B.C., Canada

INTERNATIONAL UNION OF
FORESTRY RESEARCH ORGANISATIONS

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CONE AND INSECTS
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Compiled by
Gordon E. Miller

Courtyard Inn
Victoria, B.C., Canada
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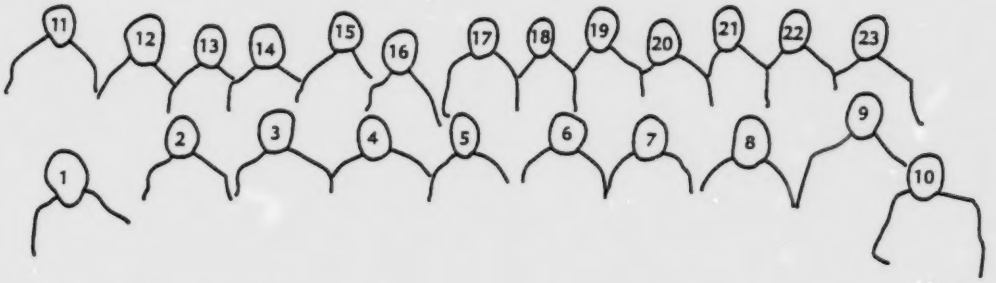

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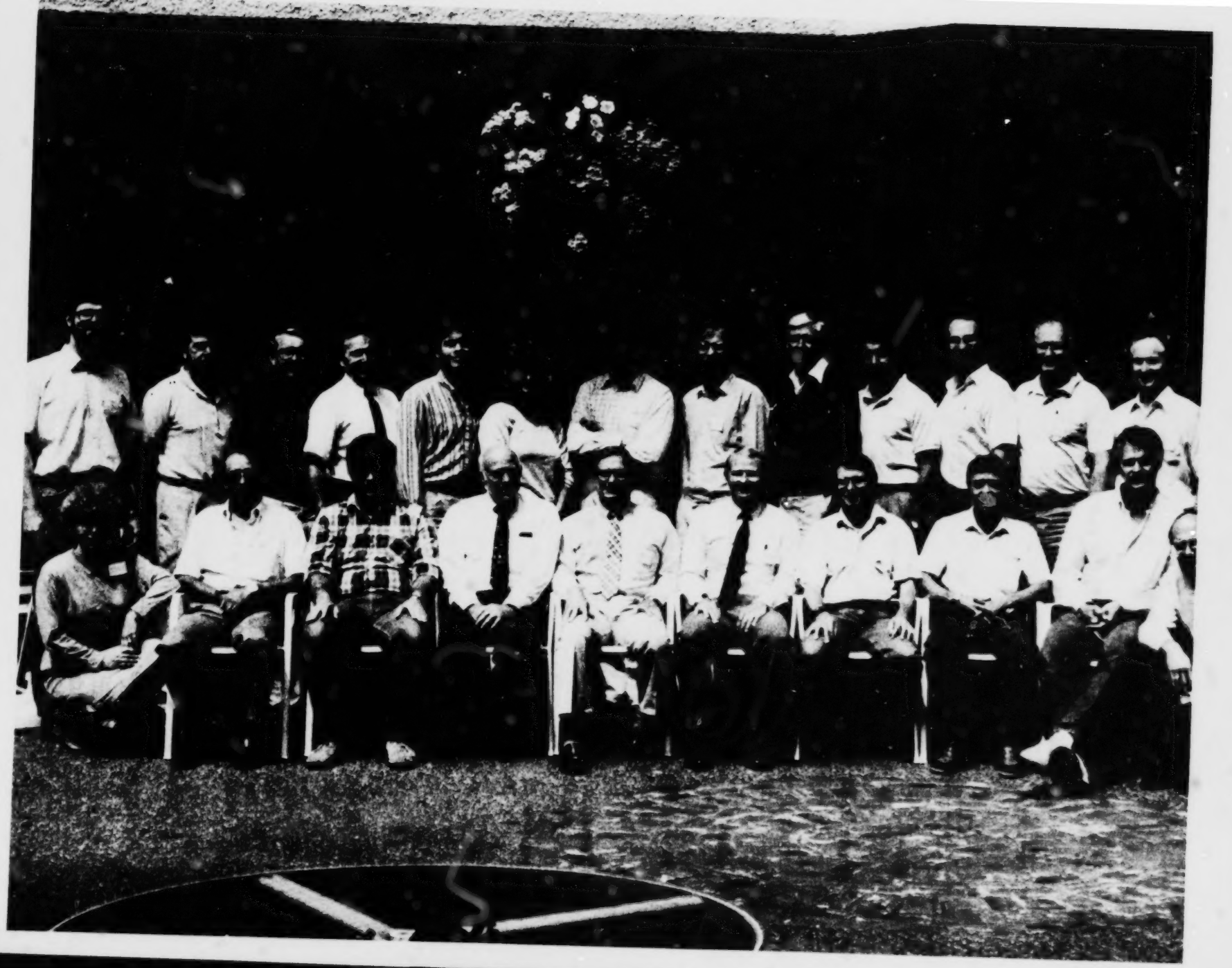

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PREFACE

The third conference of the IUFRO Working Party S2.07-01 Cone and Seed Insects took place 1988 June 26-30 at the Courtyard Inn in Victoria, B.C. The conference was co-sponsored by the International Union of Forest Research Organizations, Forestry Canada and the B.C. Forest Service. Twenty-three attendees from five countries, including Finland, France, Switzerland, the United States and Canada, registered for the meeting.

The program included the presentation of 23 technical papers in four sessions: Identification and Distribution (seven papers), Biology (seven papers), Monitoring and Damage (five papers) and Control (four papers). Three additional papers, though not presented at the conference because the authors were not able to attend, are included in the proceedings. The program also included a day-long field trip to several seed orchards on southern Vancouver Island, during which general orchard management practices as well as entomological problems were discussed. On the last day of the conference an open discussion of current research activities of the attendees was held along with the Working Party business meeting. A summary of the business meeting was published in the January 1989 Working Party Newsletter so was not included here.

Gordon Miller
Chair, Organizing Committee

TECHNICAL SESSION I:

Insect Identification and Distribution

Moderator: Dr. Alain Roques, Ardon, Olivet, FRANCE

RESULTS OF A SURVEY OF CONE AND SEED INSECTS IN SOME CONIFER FORESTS OF NORTHEAST CHINA

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Summary

A limited survey of insects susceptible to damage cones and seeds in some Conifer Forests located in Northeast China revealed a minimum of 5 species in Pinus koraiensis, 8 in Picea koraiensis, 4 in Picea jezoensis, 6 in Abies nephrolepis and 10 in Larix gmelini. 19 of the observed damage likely correspond to new records in China and some of them to new insect species. However, entomological faunas of these various trees species appear quite similar to those observed in the Far Eastern Soviet Union.

Introduction

This cooperative work has been realized in July-August 1987, to the invitation of the Northeast Forestry University in Harbin (Heilongjiang, China). Several previous studies dealt with insects damaging cones in northeast regions of China (Fung-lin Nature Protection Country, 1975; Fang et al. ,1980; Fan et al. ,1982; Zhang, 1982; Gao et al. , 1983, etc...), but many gaps subsisted, especially in tree species other than larch.

The limited duration (1 month) of this survey did not obviously allow to provide an exhaustive listing of cone and seed insects developing in Northeast Conifers. Therefore, objectives had been defined in the following way: i) to assess the relative importance of cone damage by the various species of larch cone flies (Lasiomma spp. , Fan et al. , 1982) in some characteristical larch stands located within Heilongjiang and Nei Mongol Provinces; ii) to identify possible other cone insects and their relative damage in the same larch stands; iii) to realize a preliminary survey of cone insects occuring in spruce, fir or pines tree species growing at the same location.

Comparison with insect fauna identified in cones of the same tree species within the surrounding countries will also be provided, using syntheses by Stadnitskii et al. (1978) and Kobayashi (1981) regarding the Far Eastern Soviet Union and Japan, respectively.

Location of the investigated areas and methods of collection

Figure 1 shows the location of the surveyed areas. In Heilongjiang Province, Wu-ying Natural Reserve (1), Seed Forest in Fung-lin Forest Bureau (2) and Lin-shui Natural reserve of the Northeast Forestry University (3) were investigated within the Lesser Khingan Mountains. Additional collections were performed in Botanical Garden of Heilongjiang Province (4) and Harbin Forest Farm of the Northeast Forestry University (5) , both located in Harbin City. In Nei Mongol Province, artificial and natural Larch Forests were surveyed in Yr Shi-hai (6) and Ku Du-er (7) , within the Greater Khingan Mountains.

The geographical dispersion of the investigated areas allowed to compare the result of various tree growing conditions. In the Lesser Khingan mountains, virgin forests were mainly dominated by Korean Pine (Pinus koraiensis Sieb. and Zucc.), mixed with various deciduous species (Betula spp. , Tilia spp. , Fraxinus spp. , Acer spp. ....), which forms a primary climax. To these species are added few other Conifers, like Jeddo spruce (Picea jezoensis (Sieb. and Zucc.) Carr.), Korean spruce (Picea koraiensis Nakai) , Khingan fir (Abies nephrolepis Maxim.) and Dahurian larch (Larix gmelini (Rupr.) Kusen.) . Composition of natural forests in the Greater Khingan Mountains is completely different. The association constituted by birch (Betula mandshurica) and Dahurian larch is generally dominating, accompanied in some areas by Mongolian pine (Pinus silvestris L. var. mongolica Litvin.).

The surveyed tree species were Pinus koraiensis, Picea jezoensis and P. koraiensis in (1); Larix gmelini in (2); Picea koraiensis , Pinus silvestris var. mongolica, Abies nephrolepis, Larix gmelini in (3); L. gmelini and Pinus thunbergii Parlat. in (4) and (5) , and only L. gmelini in (6) and (7).

In each larch stand, we randomly selected ten to twenty cone-bearing trees and collected ten cones from each of these latter ones. A total of 630 cones were immediatly dissected, the damage recorded and larvae put into alcohol or stored for subsequent rearings. All the characteristics of the sampled trees (altitude, location within the stand, height, exposition, cone crop, position of collected cones, density, surrounding tree species and their relative importance) were noted. Wherever it has been possible (Locations: 3, 6, 7), equal cone collections were performed in close natural and artificial stands in order to look at the results of human activity.

In the other tree species, cones were collected according to their abundance and accessibility, i. e. in small number (generally less than 15). Therefore, the single damage appearance was recorded, corresponding insects collected but the percentage of cone damage was not measured.

Most insect species were found in larval or pupal stage. Several could be reared and imagos subsequently identified. Most of the other ones, especially the young larvae, are still unidentified at a level inferior to genus or, even, family in some cases.

Insect Species and Damage observed in Cones of Conifers growing in Northeast China

Following Tables (Tables 1, 2, 3, 4) show the results we obtained tree species by tree species. The stage in which insects were collected, the presumed nature of their association with the cone, the location of the records and the existence of previous records from the Far Eastern countries have been indicated. We also mention the insect species that have not been encountered during this survey but previously known to occur in cones of similar tree species from China (Yang and Wu, 1981; Zhang, 1982; Fang, 1986; Liu, 1987), the Soviet Union (Stadnitskii et al., 1978) or Japan (Kobayashi, 1981) .

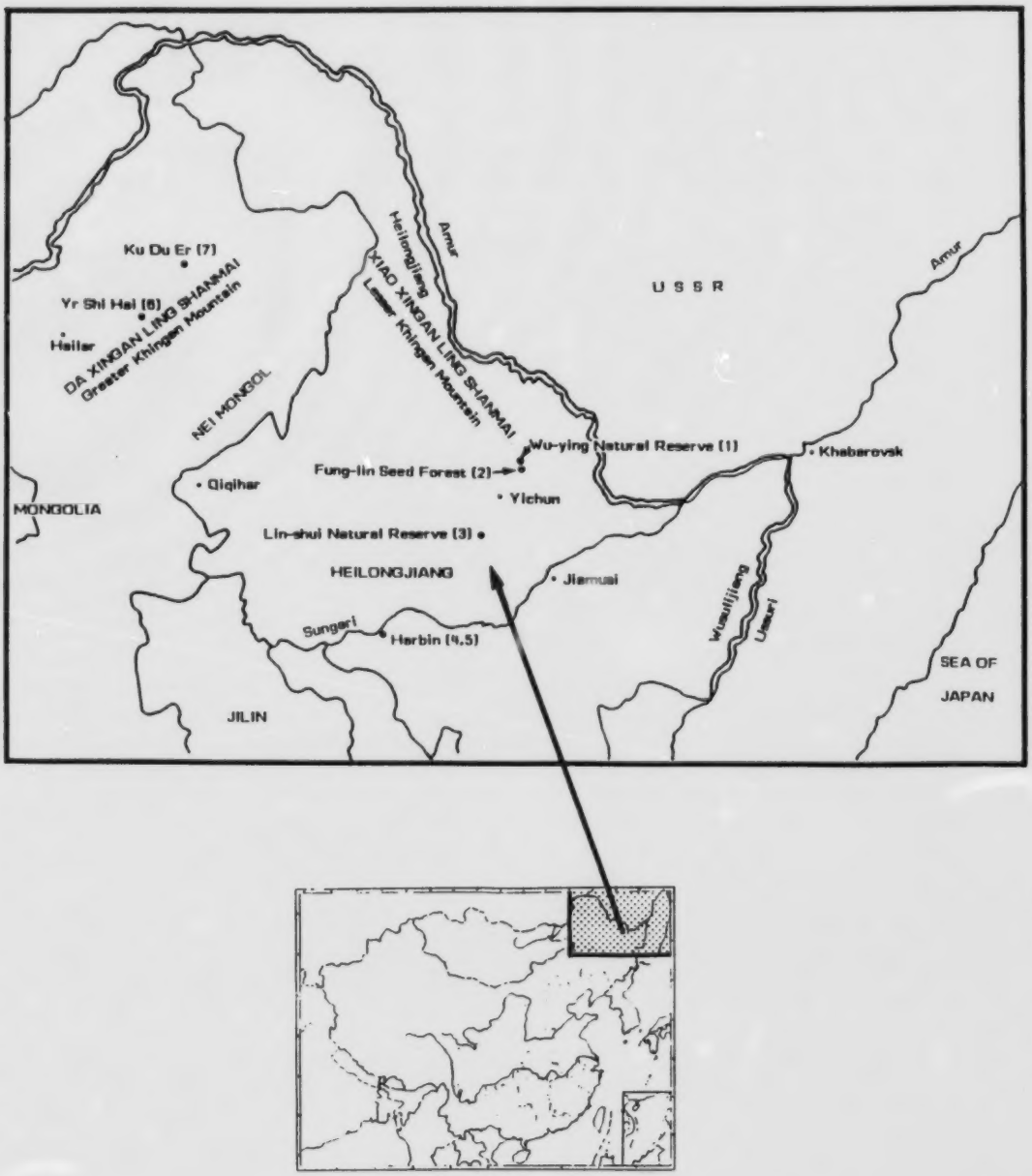

Figure 1: Location of the investigated areas in Northeastern China.

19 of the observed damage likely correspond to new records in China (5 in Pinus species, 7 in Picea species, 5 in Abies nephrolepis, 2 in Larix gmelini), though rearings and subsequent accurate identification of the corresponding insects is needed in many cases.

Pinus species (Table 1)

4 insect species new for China, at least, were found in Pinus koraiensis cones. Thus, fauna seems quite different from those observed in the Far Eastern Soviet Union and Japan. However, the dominant insect is the same, and the absence of the other species in these latter countries may be only proceeds from a limitation in the studies of P.koreana entomological complex. Conversely, presence of Petrova pini in China is probable, by reason of its range in the Far Eastern Soviet Union.
Data collected about the two other pine species are not sufficient to allow a real comparison.

Table 1: Insects and damage observed in cones of Pinus koraiensis Nakai, P. silvestris L. var. mongolica Litvin. and P. thunbergii Parlat.

Tree Species	Insect Species	Insect Stage[a] when collection	Insect-Cone[b] Relationship	Location of[c] the records	Previous Records[2] in the Far East China	USSR	Japan
Pinus koraiensis	Dioryctria abietella Den.& Schiff. f.intermediella (Pyralidae)	L[1]	CS	1	*	*	*
	Unidentified Cecidomyiidae	L	C	1	–	–	–
	Unidentified Lonchaeidae	L	Pr	1	–	–	–
	Unidentified Staphylinidae	I	Pr-Dt(?)	1	–	–	–
	Pityogenes chalcographus L. (Scolytidae)	I	dC	1	–	–	–
Pinus silvestris var.mongolica	Dioryctria abietella Den.& Schiff. f.intermediella (Pyralidae)	D	CS	3	*	*	(*)
Pinus thunbergii	Unidentified Cecidomyiidae	L	C	5	–	–	–

[1] Abbreviations: a:L=larvae, P=pupae, I=imago, D=only damage observed
b:C=damage to cone (on scales); CS=damage to cone and seeds; S=damage to seeds; WS=larvae within the seeds; Pr=predator; Dt=detritivore; dC=in dead cones.
c:cf. list in text.

[2] Previous records of other insect species in cones of the same Pinus species from the Far Eastern Soviet Union (FESU), China (C) and Japan (J) :

P.koraiensis: Petrova pini Kuzn. (Tortricidae), FESU (Kuznetsov, 1989); Gravitarmata margarotana Hein. (Tortricidae), C, J.

P.silvestris: Gravitarmata margarotana Hein., FESU, C, J; Pissodes validirostris Gyll. (Curculionidae), FESU, C.

P.thunbergii: Gravitarmata margarotana Hein., C, J; Petrova monopuncta Oku (Tortricidae), J; Petrova cristata Walsh. (Tortricidae), C, J.

Picea species (Table 2)

One of these insects (Plemeliella), that develops inside the seeds, probably is a new species. Larvae and imagos largely differ from the typical species P. abietina Seitner, known to damage seeds of spruce in Europe and in the Soviet Union (Roques, 1983). Four other insects constitute new records for China, but some have been previously noticed from the Far Eastern Soviet Union. Barbara fulgens, for instance, is an important cone pest in Khabarovsk area, just close to Heilongjiang (Stadnitskii et al., 1978).

Imagos of Resseliella and Megastigmus do not still emerge, larvae being in prolonged diapause. However, larval characteristics of Resseliella sp. look like those of R. ingrica Mam., the spruce resin gall midge known from the Soviet Union.

Table 2 : Insects and damage observed in cones of Picea koraiensis Nakai and P. jezoensis (Sieb. and Zucc.) Carr.

Tree Species	Insect Species	Insect Stage[a] when collection	Insect-Cone[b] Relationship	Location of[c] the records	Previous Records[2] in the Far East China	USSR	Japan
Picea koraiensis	Dioryctria abietella Den.& Schiff. f.intermediella (Pyralidae)	L[1]	CS	1, 3	*	*	*
	Cydia strobilella L.(Tortricidae)	L	CS	1, 3	*	*	*
	Barbara fulgens Obr.(Tortricidae)	P	CS	1(D), 3	-	*	-
	Megastigmus sp.(ezomatsuanus Huss.& Kam.?) (Torymidae)	L	WS	3	-	-	(*)
	Lasiomma sp.(anthracinum Czerny?) (Anthomyiidae)	D	CS	1	*	*	*
	Plemeliella sp.(Cecidomyiidae)	L	WS	3	-	(*)	-
	Resseliella sp.(ingrica Mam.?) (Cecidomyiidae)	L	C(S)	1, 3	-	(*)	-
	Unidentified Lonchaeidae	L	Pr	1, 3	-	-	-
Picea jezoensis	Dioryctria abietella Den.& Schiff. f.intermediella (Pyralidae)	D	CS	1	*	*	*
	Cydia strobilella L.(Tortricidae)	L	CS	1	*	*	*
	Barbara fulgens Obr.(Tortricidae)	D	CS	1	-	*	-
	Megastigmus sp.(ezomatsuanus Huss.& Kam.?) (Torymidae)	L	WS	1	-	-	(*)

[1] Abbreviations similar to those in Table 1

[2] Previous records of other insect species in cones of Picea species from the Far Eastern Soviet Union (FESU), China (C), Japan (J):
Archips oporana L.(Tortricidae), J: Choristoneura diversana Hb.(Tortricidae), C, FESU: Dioryctria schuetzeella Fuchs (Pyralidae), FESU, C: Eupithecia abietaria debrunneata Staud.(Geometridae), C, FESU, J: Megastigmus ezomatsuanus Hussey & Kamijo(Torymidae), J: Kaltenbachiola strobi Winn.(Cecidomyiidae), FESU:Resseliella ingrica Mam.(Cecidomyiidae), FESU: Plemeliella abietina Seitn.(Cecidomyiidae), FESU.

Abies nephrolepis (Table 3)

Insect Fauna also appears different from those occuring in Japan and in the Far Eastern Soviet Union. Like in Pinus koraiensis, it likely proceeds from the limited nature of the studies conducted on fir cones in these countries rather from real differences. Presence of seed insects, such as Megastigmus sp. or midges, is probable in Northeast China though not found here.

Table 3 : Insects and Damage observed in cones of Abies nephrolepis Maxim.

Tree Species	Insect Species	Insect Stage[a] when collection	Insect-Cone[b] Relationship	Location of[c] the records	Previous Records[2] in the Far East China	USSR	Japan
Abies nephrolepis	Lasiomma sp.(abietis Huck?)(Anthomyiidae)	D[1]	CS	3	–	–	*
	Dioryctria abietella Den.& Schiff. f.intermediella (Pyralidae)	L	CS	3	*	*	*
	Barbara sp.(fulgens Obr.?)(Tortricidae)	L	CS	3	–	(*)	–
	Resseliella sp.(Cecidomyiidae)	L	C	3	–	–	–
	Unidentified Lonchaeidae	L	Pr	3	–	–	–
	Unidentified Cecidomyiidae	L	C	3	–	–	–

[1]Abbreviations similar to those in Table 1

[2]Previous records of other insect species in cones of Abies species from the Far Eastern Soviet union(FESU), China(C), Japan(J) :
Eupithecia gigantea Staud.(Geometridae), C, FESU, J; Archips oporana L.(Tortricidae), J; Megastigmus boriesii Crosby(Torymidae), J.

Larix gmelini (Table 4)

Quite all the observed insect species occur in the Far Eastern Soviet Union, fewer in Japan. The Tortricidae that are already known from China but not encountered during the survey are precocious insects and likely escaped the cone before the collections began.
Discussion about the relative importance of each species will be treated in the following chapter.

Table 4 : Insects and Damage observed in cones of Larix gmelini (Rupr.) Kusen.

Tree Species	Insect Species	Insect Stage[a] when collection	Insect-Cone[b] Relationship	Location of[c] the records	Previous Records[3] in the Far East		
					China	USSR	Japan
Larix gmelini	Lasiomma laricicola Karl(Anthomyiidae)	D[1]	CS	2, 3, 4, 6, 7	*	*	*
	Lasiomma spp.[2](Anthomyiidae)	D	CS	2, 3, 6, 7	*	(*)	(*)
	Dioryctria abietella Den.& Schiff. f.intermediella (Pyralidae)	L	CS	6,7	*	*	*
	Retinia perangustana Snell.(Tortricidae)	L	CS	6, 7	*	*	–
	Resseliella sibirica Mam.(Cecidomyiidae)	L	C(S)	2, 3, 6, 7	–	*	–
	Eurytoma laricis Yano(Eurytomidae)	L	WS	3, 6, 7	*	–	*
	Unidentified Lonchaeidae	L	Pr	2, 3, 6, 7	–	–	–

[1] Abbreviations similar to those in Table 1

[2] including without possibility of accurate identification :L.melania melaniola Fan, L.luteoforceps Fan & Fang, L.baicalense Elberg, L.infrequens Ackl.,all previously known from China and from the Far Eastern Soviet Union for the two latter ones.

[3] Previous records of other insect species in cones of Larix species from the Far Eastern Soviet Union (FESU), China (C), Japan (J) :
Choristoneura diversana Hb.(Tortricidae), C, FESU: Cydia illutana H.S.(Tortricidae), FESU: Lobesia reliquana Hb.(Tortricidae), C, FESU: Lobesia aeolopa Meyrick (Tortricidae), J: Zeiraphera diniana Guénée (Tortricidae), C, FESU: Spilonota laricana Hein.(Tortricidae), C, FESU, J: Cryptoblades lariciana Mutsuura (Pyralidae), C, J: Megastigmus inamurae Yano (Torymidae), J.

Comparative damage of larch cone insects according to stand location and stand characteristics

Figure 2 shows the importance of total cone damage and the relative part played by each insect species in the 8 investigated larch stands. A significant difference in damage, as well quantitative as qualitative, appears between the stands located in the Greater Khingan Mountains and the ones from the Lesser Khingan Mountains. Quite all the cones are damaged by the joint action of a large complex of phytophages in the former stands whereas only half of the cones are attacked by a group apparently reduced to its dipterous components in the latter ones. However, no difference in damage or fauna composition is noticeable between artificial and natural forest located in the same area. A further study dealing with the possible influence of peculiar stand characteristics, like tree density, will be performed in a short time.

Larch cone flies represent the dominant species in all cases, damaging 480 of the 630 examined cones (i. e. 76,2%) and tending to occupate the whole available habitat in Nei Mongol stands. Respective damage to be attributed to each Lasiomma species is difficult to ascertain, excepted from L.laricicola, whose larvae characteristically destroy cone axis. However, the part played by this species in Lasiomma complex is reduced, its damage generally representing less than 13% of Lasiomma total damage.

Figure 2: Total Cone Damage and Relative Importance of each Insect Species in the 8 surveyed Larch Stands. (AF: Artificial forest: VF: Virgin Forest). Insect Species: LL: Lasiomma laricicola: Lspp.: Other Lasiomma species: DA: Dioryctria abietella f.intermediella: RP: Retinia perangustana: RS: Reseliella sibirica: EL: Eurytoma laricis.

L.melania melaniola spirals round t axis near the cone basis whereas L. infrequens generally occurs in the apical part, but damage by these insects could be confused with those, still unknown, by L. baicalense and L. luteoforceps. A typology of cone damage by Lasiomma spp. is under study, using multivariate analysis performed after digitalization of the drawings corresponding to damage zonation in the 480 attacked cones that have been examined.

The second species in importance is the tortricid Retinia perangustana, that is strictly related to larch. Though its known distribution covers Nei Mongol, Jilin and Heilongjiang Provinces in China (Liu, 1987) , it has been observed in the single Nei Mongol stands. This observation links up the records from Stadnitskii et al. (1978) who noticed its relative scarcity in Khabarovsk area, close to Heilongjiang, conversely to its abundance in the Amguni River Basin, just northern to Nei Mongol. Damage appearance is similar to the one observed in Europe (Roques, 1983) , with irregular galleries distant from the axis. Only one larva generally develops per cone, but it often seems exclusive of Lasiomma spp. occurence.

The cone pyralid Dioryctria abietella f. intermediella is both more polyphagous (cf. Tables 1, 2, 3) and less important in larch cones, never colonizing more than 10% of them. Its damage is easily distinguishable, clear dejections generally existing from the apical part of the cone. A maximum of 3 larvae has been observed in a single cone.

Larvae of the midge Resseliella sibirica (= Thomasiniana sibirica Mam. = Camptomyia laricis Mam.) have been observed in all the stands, generally accompanying Lasiomma damage. These small larvae are at first of whitish or yellowish color and turn orange at maturity. They develop on the internal side of the scales, near or on the seeds. Scales tissues are consumed and, consequently, corresponding seeds abort. We observed 1 to 12 larvae per cone. They begin to leave the cones from late July to pupate in the litter. Though this insect colonizes up to 17% of the cones in some cases, its economic significance appears still limited in relation to larval habits. However, an accurate survey of the Northeastern larch stands is needed, in regard to data from the Far Eastern Soviet Union. Stadnitskii et al. (1978) considered this species to damage about half of the seeds when 15-25 larvae are present per cone, that occurs in some places.

The japanese seed eurytomid, Eurytoma laricis, develops within the seeds. It was therefore difficult to estimate its real damage, without using X-ray treatments. It was previously known to infect seeds of Larix leptolepis (Sieb. and Zucc.) Gord., L. principis rupprechtii Pilg. and L. gmelini in China, especially in Nei Mongol where Gao et al.(1983) estimated its damage to reach 27.9% at a maximum, 10% on the average. We found one larva in the Lesser Khingan Mountains (2), thus establishing its presence in this area.

Conclusion

Several cone insect species new for China where discovered during this preliminary survey, that was necessarily superficial. This shows all the possibilities offered to cone insect studies in this country.

Most of these species were previously known from the Far Eastern Soviet Union and consequently the fauna of Northeast China appears very similar to that of this region. Absence of real natural frontier between these two geographically close regions easily explains this observation. Conversely, some differences exist with Japan fauna. In this viewpoint, the lepidopterous fauna of cones seems more homogeneous in the Far Eastern countries than both the chalcid and dipterous ones.

However, our actual knowledge does not allow to understand if it corresponds to real differences or gaps in corresponding studies.

In conclusion, we suggest a peculiar attention to identification of insects whose larvae strictly develop in coniferous seeds in Northeastern Asia.

References

Fan Zi-de, Ge Feng-Xiang, Zhang Run-sen and Fang San-yang, 1982. (On chinese species of Lasiomma especially those injurious to the Coniferous cones (Diptera:Anthomyiidae))(In chinese). J.Northeastern For.Inst., 1:1-12.

Fang San-yang, Fan Tze-teh, Wang Chang-san and Shu Cheng-hwa, 1980. (Studies on the components of species group of genus Lasiomma and bionomics of species which injure larch cones in Wu-ying district of Heilongjiang Province). (In chinese). J.Northeastern For.Inst., 2:39-46.

Fang San-yang, 1986. A review of Tree Cone and Seed Pests in China. In: Proc. 2nd Internat. Conf. Cone and Seed Insects WP. IUFRO S2. 07-01. Briançon. 3-5 September 1986. A. Roques(Ed.). INRA. Versailles (France). 59--64.

Fung-lin Nature Protection Country, 1975. (Preliminary observations on Dioryctria abietella Schiff.) (In chinese). Kunchong Zhishi, 1: 34-35.

Gao Bu-qu, Xu Shan-bin, Zhang Rong, Li Chu-seng and Zhang Li-guang, 1983. (Study on bio-ecological characters of Japanese larch Eurytomid (Eurytoma laricis Yano)). (In chinese). J.Northeastern For.Inst., 11, (3): 51-56.

Kobayashi K., 1981. Cone and seed insects of Japanese Conifers. In: Proc. For. Plant & For. Protect., XVII IUFRO World Congr., Div. 2, Kyoto, Japan, 455-461

Kuznetsov, V.I., 1969. New eastern asiatic species of leaf rollers (Lepidoptera, Tortricidae). Entomol. Rev., 2:206-218.

Liu You-quiao, 1987. (Microlepidoptera feeding on fruits and seeds of woody plants in China). (In chinese). Forest pest and disease, (1), 30-35.

Roques A., 1983. Les insectes ravageurs des cônes et graines de Conifères en France. INRA, 135 pp.

Stadnitskii G.W., G.I. Iurchenko, A.N. Smetanin, V.P. Grebenshchikova and M.V. Pribylova, 1978. (Cone and Seed Pests of Conifers). (In russian). Moscou : Lesnaia promyshlennost, 168 pp.

Yang Xiu-yuan and Wu Jian, 1981. (A checklist of the forest insects in China). (In chinese). The Chinese Academy of Forestry. Forest Research Institute, Beijing, China, 444 pp.

Zhang Shi-min, 1982. (Study on the cone seed pests of different needle-leaved forest types in natural forests). (In chinese). J. Northeastern For. Inst., 3, 21-27.

DISTRIBUTION AND HOST PLANTS IN SOME SPECIES OF GENUS DIORYCTRIA ZELLER IN CHINA

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1 - Dioryctria sylvestrella (Ratzeburg, 1840)

Distribution : Heilongjiang (North-East China).
Host : Pinus sylvestris mongolica Litv.

2 - Dioryctria rubella Hampson, 1901

Distribution : Heilongjiang, Liaoning, Jilin (North-East China), Hebei (North China), Shandong, Jiangsu, Jiangxi, Zhejiang, Anhui, Fujian (East China), Hunan (Central China), Guangdong, Guangxi (South China), Sichuan (West China), and Yunnan (South-West China).
Host : Pinus tabulaeformis Carr., P. densiflora Sieb. et Zucc., P. sylvestris mongolica Litv., P. thunbergii Parl., P. massoniana Lambert, P. yunnanensis Franch., P. armandii Franch., P. hwangshanensis Hsia, P. wallichiana Jackson, P. elliotii Engelm., and Picea asperata Mast.

3 - Dioryctria yuennanella Caradja, 1937

Distribution : Yunnan.
Host : Pinus armandii Franch.

4 - Dioryctria kunmingella Wang et Sung, 1985

Distribution : Yunnan.
Host : Pinus yunnanensis Franch.

5 - Dioryctria magnifica Munroe, 1958

Distribution : Shaanxi (West China).
Host : Abies magnifica Marr.

6 - Dioryctria abietella (Denis et Schiffermüller, 1775)

Distribution : Heilongjiang, Shaanxi, and Yunnan.
Host : Pinus yunnanensis Franchet, P. armandii Franchet, P. koraiensis Sieb. et Zucc., and Abies magnifica Marr.

7 - Dioryctria assamensis Mutuura, 1971

Distribution : Shaanxi, Tibet (Himalaya).
Host : Pinus khasya Royale.

8 - Dioryctria mutatella Fuchs, 1903

Distribution : Jiangsu, Zhejiang, Fujian, Yunnan, and Sichuan.
Host : Pinus massoniana Lambert, P. yunnanensis Franchet, P. armandii Franchet, and P. taeda L.

9 - Dioryctria schuetzeella Fuchs, 1899

Distribution : Heilongjiang, Jilin, Liaoning, and Ningxia (North-East China).
Host : Picea koraiensis Nakai.

10 - Dioryctria pryeri Ragonot, 1893

Distribution : Heilongjiang, Liaoning, Hebei, and Shaanxi.
Host : Pinus tabulaeformis Carr., and P. densiflora Sied. et Zucc.

11 - Dioryctria yiai Mutuura, 1972

Distribution : Hebei, Hunan, Jiangxi, Sichuan, and Guangdong.
Host : Pinus massoniana Lambert, and P. tabulaeformis Carr.

12 - Dioryctria castanea Bradley, 1969

Distribution : Tibet.
Host : Pinus insularis Endlicher.

Figure 1 shows the location of the corresponding records throughout the People's Republic of China.

Figure 1 : Distribution of some Dioryctria species in China

○ D. sylvestrella
● D. rubella
✱ D. yuennanella
✱ D. kunmingella
☆ D. magnifica
▲ D. abietella
△ D. mutatella
★ D. assamensis
♦ D. castanea
■ D. pryeri
★ D. yiai
□ D. schuetzeella

BIOSYSTEMATICS OF CONOPHTHORUS (COLEOPTERA: SCOLYTIDAE) IN EASTERN NORTH AMERICA

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ABSTRACT

The cone beetles in the genus Conophthorus are serious seed pests of many species of pines in North America. Fifteen species of Conophthorus are currently recognized but several problems in the taxonomy exist: (1) many species are very difficult to distinguish on the basis of anatomical characters alone because these characters are poorly developed and variable, (2) several sibling species are suspected in the western forms but detailed studies must be done to before they can be recognized, and (3) two sibling species (C. banksianae McPherson and C. resinosae Hopkins) that occur in eastern North America are recognized but it is suspected that they may actually represent one species. My study examines the latter problem. Preliminary analysis of the biosystematic study reveals that: (1) C. banksianae is not apparently bivoltine but is univoltine like C. resinosae, (2) the two sibling species have similar electrophoretic profiles and are distinct from C. coniperda, (3) the two sibling species have the same chromosome number and morphology, and again C. coniperda is distinct from them, (4) both sibling species will attack red and jack pine cones and shoots in choice and no choice tests, but there is a distinct preference of C. banksianae for jack pine shoots and C. resinosae for red pine cones, and (5) the male genitalia do not provide taxonomic characters that would separate the three species. The preliminary analysis suggests that the validity of C. banksianae as a species separate from C. resinosae can be seriously questioned and that the species may be synonomized when the study has been completed.

INSECT DAMAGE TO WESTERN LARCH CONES AND SEEDS IN THE UNITED STATES

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SUMMARY

A five year study was begun in 1985 to determine factors decreasing western larch cone production at thirteen sites in Montana, Idaho, Oregon, and Washington. Frost and insects were the major causes of cone and seed loss in 1985, 1986, and 1987. Insects identified from cone dissections and rearing include the larch cone maggot (Diptera: Anthomyiidae), western spruce budworm (Choristoneura occidentalis Freeman Lepidoptera: Tortricidae), a woolly adelgid (Adelges viridis = A. strobilobius Ratzeburg Homoptera: Phylloxeridae), and cone scale midges (Resseliella sp. Diptera: Cecidomyiidae).

INTRODUCTION

Western larch (Larix occidentalis Nutt.) grows within the Upper Columbia River Basin of southeastern British Columbia, northwestern Montana, north and west-central Idaho, and northeastern Washington; along the eastern slopes of the Cascade Mountains in south-central Washington and north-central Oregon; and in the Wallowa and Blue Mountains of southeastern Washington and northeastern Oregon (Schmidt et al. 1976). Few cones have matured for many years within much of the range of larch in the United States, except for the forests near the Canadian border in eastern Washington and Idaho and much of northwestern Montana. Reasons for low cone production are uncertain, but we know that insects can cause heavy damage to western larch cones and seeds (Shearer 1984), and probably reduce the potential cone crop most years.

A 5-year study began in 1985 to determine factors decreasing larch cone production at 11 sites in northern Idaho and adjacent western Montana. In 1987, this study was expanded to include two additional sites near the western extreme of the range of larch in Washington and Oregon. Another site, in the Blue Mountains of Oregon, was added in 1988. During the 1985 and 1986 field

seasons, insects were field identified to family and, where possible, to genera; species identification was omitted. But in 1987 a cooperative study provided positive identification of several insects.

In 1985 and 1986, frost and insects eliminated or greatly reduced the cone potential (Shearer and Theroux 1986). Shearer and Theroux's (1986) paper also reviewed the insects causing damage to western larch cones and seeds. The purpose of this paper is to identify the insects feeding on larch cones and seeds in 1987, to describe the damage, and to indicate its seriousness in terms of cone and seed loss.

EXPERIMENTAL METHODS

Study Areas and Sample Trees

Within the range of western larch in the United States, two study sites were selected in Oregon, one in Washington, nine in Idaho, and two in Montana (fig. 1). These stands originated after wildfires and are now 50 to 100 years in age. At each study area, 10 open-growing dominant or codominant larch were selected for study (except only five at the Savage Camp). Three criteria were used to select the sample trees: (1) crown length at least 40% of total tree height, (2) accessible for climbing, and (3) evidence of prior cone production. These trees were climbed using a combination of tree climbing ladders (first 6 m), steps attached to the open bole (top of ladder to lowest live branches), and free climbing on live branches (to 9 cm bole diameter). The living crown was divided into thirds and the number of branches originating at the bole within each third was recorded.

Cone Production and Development

At the first visit to each stand in the spring, the five sample trees with the greatest number of seed cones (determined from binocular estimates from the ground) were climbed to make a more precise cone count. A total branch count was made by crown thirds, then the number of cones (living and dead) were counted on six randomly selected branches--two from each third of the crown. If two branches with new cones were not found in one third of the crown, they were marked in another third, so that a total of six branches were sampled. The number of potential cones on each tree was estimated by multiplying the average number of cones-per-branch sample by the total number of cone-bearing branches.

Development of 25 marked cones was recorded at each visit on the two larch sample trees that had the greatest cone potential at each location. These cones were close enough to the observer so the length and external condition could be determined and dead cones could be removed without bending the branches. No more than five cones were marked on any branch. Most marked cones were in the upper third of the crown where the branches were shortest.

Cone survival was estimated by counting the mature cones on the six randomly selected branches on each of the five sample trees. Cone mortality was the difference between the total cone count obtained during the first visit and the surviving cones in late August.

Figure 1.--Distribution of 14 study areas within the natural range of western larch.

Collection, Rearing, and Identification

Cones were collected by USFS personnel at all study sites where adequate cones were produced and were shipped by express mail to the Forest Pest Management Laboratory at Utah State University. Collections were made during the regular visits to study sites by USFS and from two to four samples were received from 9 sites during the 1987 field season. Each sample received at USU was divided into two equal groups of cones; one group was dissected to document damage and the other was placed in a rearing container to obtain adult specimens for identification.

From dissections the immatures and their damage were characterized by notes and drawings. Percentages of cones and seeds damaged by each insect observed were tabulated in dissection notes. Photographs were made of typical damage and immature forms of the insects observed.

Rearing was done to obtain adult specimens for identification. Samples placed in rearing containers at room temperature were checked daily for emergence of adult insects. Adults were collected and handled in a standard manner and shipped to taxonomists specializing in the particular insect family.

RESULTS

Study Areas and Sample Trees

A summary of the 11 study areas in Idaho and Montana was given by Shearer and Theroux (1986) but not of the three study areas in Oregon and Washington. A description of all 14 sites by state is given in table 1. The study areas range in latitude from 44°29′ to 48°46′ N. (a distance of 471 km), in longitude from 114°28′ to 121°35′W. (a distance of 459 km), and in elevation from 762 to 1768 m. The western larch sample trees varied in age from 47 to 98 years in 1987. They ranged in height from 21.6 to 30.6 m and in diameter at 1.4 m from 25.1 to 43.3 cm. The number of live branches originating at the bole varied from 111 to 142. Length of the living crown extended from 41% to 68% of the total height of the study trees.

Cone Production and Development

Nearly all the sample trees produced seed cone buds each year (Table 2). But there was a wide range in the number of seed cone buds produced within the sample trees as well as between the stands. For those stands that have been measured 3 years, Meadow has produced an average of more than 2000 cones per tree per year; Peter, Beacon, and Ericson an average of between 900 and 1000 cones per tree per year; Twin, Brush, and Twelve Mile an average of between 250 and 400 cones per tree per year; and Savage and Standard an average of less than 100 cones per tree per year.

Cones develop quickly after bud bursts and elongation is finished in early July. Cone maturity usually occurs in mid-August when embryos are fully elongated.

Table 1. Location; elevation; and average age, height, diameter, and branches in Montana and Idaho (1984) and in Oregon and Washington (1987) of the 10 western larch sample trees at each study area (only five at Savage).

Study area	Location		Elevation	Average			
	North lat.	West long.		Age[1]	Total height	Diameter at 1.4 m	Live branches[2]
			(m)	(Yr)	(m)	(cm)	(No.)
IDAHO							
Meadow	48°46′	116°14′	762	80	27.3	33.8	135
Twin	48°04′	116°09′	853	82	30.2	39.1	111
Beacon	47°27′	115°40′	1189	83	30.6	38.4	135
Cairn	47°22′	115°52′	1372	[3]58	27.4	42.1	141
Brushy Fork	46°37′	114°28′	1463	[3]78	27.7	37.6	142
Savage	46°29′	115°32′	1463	46	23.9	32.5	125
Ericson	45°54′	115°29′	1433	55	23.2	34.0	140
Peter	45°39′	116°03′	1768	64	23.4	33.0	117
Brush Mtn.	45°09′	116°22′	1524	63	24.0	34.0	127
MONTANA							
Standard	48°04′	115°31′	1097	68	21.6	25.1	129
Twelve Mile	47°28′	115°17′	1372	65	23.2	28.2	127
OREGON							
Catherine	45°06′	117°40′	1345	47	25.1	38.8	198
Crystal	44°29′	120°24′	1463	98	27.3	43.3	65
WASHINGTON							
Sleeping	46°04′	121°35′	820	70	29.0	41.4	108

[1] Age at about 15 cm above average ground level.

[2] Branches that originate at the bole.

[3] Age at 1.37 m (age at 15 cm not taken).

Table 2. Average number of cones per study tree and their range by study area, estimated soon after bud opening in 1985-1987.

Study area	1985			1986			1987		
	Cones	Range	n	Cones	Range	n	Cones	Range	n
	(No.)			(No.)			(No.)		
IDAHO									
Meadow	1220	416-2288	5	2879	892-6137	5	2069	1136-2939	5
Twin	656	304-1232	5	56	9- 160	5	465	187- 762	5
Beacon	828	471-1082	5	1354	36-4039	10	720	201-1933	10
Cairn	1			322	2- 688	10	162	42- 254	5
Brushy Fork	1			284	0-1722	10	1915	176-3099	5
Savage	163	0- 736	5	111	0- 512	5	1	0- 6	5
Ericson	981	121-1937	5	1527	553-2383	5	300	34- 454	5
Peter	1270	366-2795	5	1181	178-2275	5	483	0- 906	6
Brush Mtn.	318	75-1029	5	485	81-1316	5	155	100- 264	5
MONTANA									
Standard	199	1- 432	5	24	3- 58	5	22	1- 48	5
Twelve Mile	267	42- 563	5	287	76- 957	5	201	49- 402	5
OREGON									
Catherine	1			1			1		
Crystal	1			1			1534	852-2312	5
WASHINGTON									
Sleeping	1			1			1677	216-3661	9

[1] Not established, no data collected.

Collection, Rearing and Identification

Four major seed and cone insects have been identified from collections and rearings of cones of western larch. Two have been identified to species, one to genus and one to family only. Table 3 summarizes the infestation levels of the three major species encountered.

The western spruce budworm (Choristoneura occidentalis Freeman; Lepidoptera: Tortricidae) is a widely recognized defoliator of western conifers and has been previously described on the cones of western larch (Dewey and Jenkins 1982). No special taxonomic work was required to identify this insect. Western spruce budworm is most significant on the Brush Mtn. study area on the Payette National Forest and at the Crystal study area on the Ochoco National Forest.

Adelges viridis (= A. strobilobius Ratzeburg (Homoptera: Phylloxeridae) is an insect that occurs in great masses on the surface of conelets in the early spring. It is difficult to quantify impact, but we will attempt to correlate its activity to cone size, seed number and viability in the coming season.

The larch cone maggot (Diptera: Anthomyiidae) is wide spread throughout the study area and is considered to be the major larch cone feeding insect. The genus containing cone maggots is presently being revised and little taxonomic work has been done on American species. Adult specimens collected in the field have been identified as seed feeding Anthomyiidae, but not in the species anthracina and probably a new species. Cone maggots have previously been described in Hylemya (Hedlin et al. 1980) in America and Lasiomma in Europe (Rogues et al. 1984). The maggot overwinters as pupae emerging as adults the following spring.

Scale midges (Resseliella sp. Diptera: Cecidomyiidae) have been collected at several sites, but cause only minor localized damage to relatively fev seeds. Adults are being reared for identification to species.

DISCUSSION

The major factors decreasing western larch cone production have been identified as frost and cone and seed feeding insects including western spruce budworm, the larch cone maggot, cone scale midges, and woolly adelgids. Frost damage continues to be significant and again in 1988 considerable frost mortality occurred at many of the sites.

Research is currently being conducted to further describe life histories of the major insect pests and to develop methods on control. Diptera studies include making detailed biological observations of the midges and maggots and determining degree day thresholds for emergence. We are also conducting experiments to describe host selection and flight behavior of cone maggots using a design similar to that developed by Rogues (1986). Laboratory methods are being employed to develop means of efficiently rearing midges and maggots to adults.

Table 3. Percent cones infested by species on each collection date in 1987.

Study area	[1]WA				CM				WSB			
	[2]I	II	III	IV	I	II	III	IV	I	II	III	IV
IDAHO												
Meadow	90	100	100	100	15	60	90	50	0	10	0	10
Twin	90	100	100	90	0	0	10	50	0	0	0	0
Beacon	80	100	100	90	0	0	13	0	0	0	0	0
Ericson	20	60	40	80	0	20	0	0	10	0	0	0
Peter	15	100	100	-	0	0	50	-	0	10	10	-
Brush Mtn.	80	-	-	-	0	-	-	-	80	-	-	-
Carin	10	100	100	-	0	0	0	-	0	0	0	-
OREGON												
Crystal	100	65	65	72	0	40	25	30	20	92	75	83
WASHINGTON												
Sleeping	80	80	64	100	25	40	72	20	0	0	47	0

[1] WA = woolly adelgid, CM = cone maggot, WSB = western spruce budworm
[2] I= , II= , III= , IV=

We are attempting to assess the impact of adelgids on seed production by bagging cone-bearing branches prior to adelgid appearance on cones. Bagged cones will be compared to unbagged cones to evaluate the effect of adelgid feeding on seed number, size, and viability.

Insecticide tests are being conducted to the effectiveness of acephate implants as a function of application rate and timing for control of cone maggot and western spruce budworm.

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LITERATURE CITED

Hedlin, A., H. Yates, D. Tovar, B. Ebel, T. Koerber, and E. Merkel. 1980. Cone and seed insects of North American conifers. Canad. Forest. Serv. USDA Forest Serv., Sec. de Agric., Mexico. 122 pp.

Rogues, A., J. P. Raimbault, and A. Delplanque. 1984. Les Dipteres Anthomyiidae de genre Lasiomma Stein ravageurs des cones et graines de Meleze d'Europe (Larix decidua Mill.) en France. II. Cycles biologiques et degats. Zeitschrift f. angewandte Entomologie 4:350-367.

Rogues, A. 1986. Responses des adultes de Lasiomma melania, ravageur des cones de Larix decidua, a des pieges colores de differents types. Entomol. exp. appl. 40:177-187.

Schmidt, W. C., Shearer, R. C., and Roe, A. L. 1976. Ecology and silviculture of western larch forests. U.S. Department of Agriculture Tech. Bull. 1520, 96 pp.

Shearer, R. C. 1984. Influence of insects on Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, and western larch, Larix occidentalis Nutt., cone and seed production in western Montana. IUFRO Working Party: S2.07-01. Cone and Seed Insects Symposium, Athens, Georgia, pp. 112-121.

Shearer, R. C. and Theroux, L. J. 1986. Insects and frost limit cone production of Larix occidentalis Nutt. IUFRO Working Party: S2.07-01. Cone and Seed Insects Symposium, Briancon, France, pp. 205-215.

The relative importance of cone and seed insect species on commercially important conifers in British Columbia

by

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Abstract

The results of an on-going survey of cone and seed insects in British Columbia are reported. Conifers which frequently suffered heavy seed losses included Abies amabilis, A. grandis, Picea engelmanni, P. glauca, P. mariana and Pseudotsuga menziesii; Pinus ponderosa suffered moderate losses; Larix occidentalis, Picea sitchensis, Pinus monticola, Thuja plicata suffered generally light with occasionally heavy losses; and Pinus contorta, Tsuga heterophylla and T. mertensiana suffered minimal losses.

The common cone and seed insect species and the relative importance of each are indicated for each species of conifer. The most important pests on conifers frequently suffering heavy losses were Strobilomyia neanthracina and Cydia strobilella on the spruces; Barbara colfaxiana and Contarinia oregonensis on Douglas-fir; and Earomyia spp., Megastigmus spp., and Dasineura spp. on true firs.

Résumé

Les auteurs font un compte rendu sur une étude permanente des insectes qui s'attaquent aux cônes et aux graines de conifères en Colombie-Britannique. Les conifères qui perdent fréquemmont de grosses quantités de graines sont l'abies amabilis, l'A. grandis, le Picea engelmanni, le P. glauca, le P. mariana et le Pseudotsuga menziesii; le Pinus ponderosa a subi des pertes modérées; le Larix occidentalis, le Picea sitchensis, le Pinus monticola, le Thuja plicata ont connu quelques pertes lourdes, mais les pertes sont en général assez faibles; le Pinus contorta, la Tsuga heterophylla et la T. mertensiana n'ont subi que des pertes mincures.

Les insectes communs des cônes et des graines et leur importance relative sont indiquées pour chaque espèce de conifère. Les espèces d'insectes nuisibles qu'on retrouve le plus fréquemment sur les conifères subissant fréquemment de lourdes pertes sont la Strobilomya neanthracina et la Cydia strobilella sur les épinettes, la Barbara colfaxiana et la Contarinia oregonensis sur les Douglas, et la Earomya, le Megastigmus et la Dasineura sur les sapins.

Introduction

Many species of cone and seed insects are known from B.C. (Hedlin 1974; Hedlin et al. 1980). Few surveys of seed losses to these insects have been reported; although two longer-term studies have been carried out on Douglas-fir (Hedlin

1964a; Miller et al. 1984). Losses have been reported in association with studies on pest biology and insecticide trials but these have typically been for one or two years and at few sites.

The Forest Insect and Disease Survey and researchers at the Pacific Forestry Centre have been making collections of cones for identification of pests and quantification of losses in all commercial conifers in B.C. for many years; in the case of Douglas-fir in coastal areas, for more than 30 years. However, most of the collections, particularly for those from the interior regions of B.C., have been made since 1970. The results of this survey are reported herein.

Methods

The survey has not been carried out systematically. Rather, as opportunities have arisen based on availability of cones and resources for sampling, collections have been made from a variable number of sites each year. The number of sites (a site is defined as one stand sampled in one year) and associated numbers of cones sampled for each species of conifer are listed in Table 1. The number of trees and cones per site have varied considerably, ranging from 1 to 20 trees and 10 to 168 cones per tree, primarily being influenced by cone crop size, i.e., larger collections were made when large crops occurred. Only sites where at least two trees and 20 cones were collected have been included in the data summaries reported here. Generally, cones were collected from a minimum of two or three branches per tree from the lower portion of cone-bearing crowns. Yellow cypress, Chamaecyparis nootkatensis (D. Don) Spach, was the only major commercial conifer not included in the survey.

During cone processing, at least 20 cones were randomly selected from the collection for each site. Each cone was sliced along its axis (Winjum and Johnson 1960). The numbers of filled seeds and seeds damaged by individual insect species were counted on one cut surface.

Results

Losses to cone and seed insects, relative to the numbers of filled seeds produced per cone, have varied dramatically among conifers (Table 1). Several conifers have lost on average as many seeds to insects as they have produced whereas in others losses have been minimal. Conifers which suffer heavy losses to cone and seed insects include Douglas-fir, white spruce, Engelmann spruce, black spruce, Pacific silver fir, grand fir, and subalpine fir. Moderate losses have occurred consistently in ponderosa pine. The apparently moderate losses in Sitka spruce, western redcedar, western white pine and western larch resulted from generally light losses with occasional heavy losses. Lodgepole pine, western hemlock and mountain hemlock have suffered little loss.

The complexes of insects commonly found damaging seed ranged from eight on grand fir to one on western larch (Table 2). With respect to relative

Table 1. Sample size and overall average number (range of averages per site) of filled and damaged seeds per cone

Conifer	No. sites	No. cones	Seeds per cone	
			filled	damaged
Pacific silver fir (*Abies amabilis*)	17	374	9.3 (4.0–18.0)	5.3 (0–23.6)
Grand fir (*A. grandis*)	9	135	4.5 (0–16.4)	8.8 (0–35.2)
Subalpine fir (*A. lasiocarpa*)	49	3009	9.6 (0–37.3)	2.7 (0–33.1)
Western larch (*Larix occidentalis*)	17	367	2.9 (0.1–5.9)	0.6 (0–3.2)
Engelmann spruce (*Picea engelmanni*)	133	3821	3.8 (0–15.8)	4.0 (0–19.7)
White spruce (*P. glauca*)	167	5107	3.9 (0–20.0)	3.7 (0–17.0)
Black spruce (*P. mariana*)	15	350	1.4 (0–6.9)	0.9 (0–7.2)
Sitka spruce (*P. sitchensis*)	57	1378	3.9 (0–9.2)	1.6 (0–16.2)
Lodgepole pine (*Pinus contorta*)	32	718	2.4 (0.8–5.3)	<0.1
Western white pine (*P. monticola*)	7	107	7.7 (0.7–16.0)	2.7 (0–13.0)
Ponderosa pine (*P. ponderosa*)	13	297	5.6 (0.2–12.6)	2.5 (0–6.2)
Douglas-fir (*Pseudotsuga menziesii*)	349	27572	3.7 (0–12.7)	2.4 (0–20.6)
Western redcedar (*Thuja plicata*)	22	420	1.2 (0–2.7)	0.3 (0–2.0)
Western hemlock (*Tsuga heterophylla*)	39	871	2.5 (0.1–5.4)	<0.1
Mountain hemlock (*T. mertensiana*)	8	165	6.0 (2.5–8.7)	0.4 (0–1.8)

Table 2. For each conifer, average percentage of the total damaged seeds per cone caused by each insect in the six forest regi of British Columbia. The number of sites with insect damage in each region are in parentheses.

Conifer	Insect	Overall	Vancouver	Prince Rupert	Prince George	Cariboo	Kamloops	Nelson
Pacific silver fir	Dasineura abiesema Foote (3)*	31	34 (15)	10 (2)	-	-	-	-
	Megastigmus lasiocarpae Crosby (5)	24	21	47	-	-	-	-
	Dasineura sp. (gall midge) (3)	21	21	16	-	-	-	-
	Barbara sp. (7)	13	14	<1	-	-	-	-
	Earomyia abietum McAlpine (4)	9	9	9	-	-	-	-
	Dioryctria abietivorella (Grote) (6)	2	<1	18	-	-	-	-
Grand fir	Earomyia abietum McAlpine & Earomyia sp. (4)	32	26 (6)	-	-	-	-	53 (2)
	Dasineura sp. (gall midge) (3)	26	34	-	-	-	-	<1
	Dasineura abiesemia Foote (3)	15	19	-	-	-	-	0
	Barbara sp. (7)	12	11	-	-	-	-	17
	Megastigmus pinus pinus Parfitt & M. rafni Hoffmeyer (5)	8	11	-	-	-	-	2
	Dioryctria abietivorella (Grote) (6)	7	0	-	-	-	-	28
Subalpine fir	Earomyia abietum McAlpine (4)	32	22 (2)	12 (18)	26 (6)	35 (3)	45 (9)	59 (10)
	Megastigmus lasiocarpae Crosby (5)	29	20	49	17	3	16	19
	Dasineura abiesemia Foote (3)	24	32	17	56	6	21	22
	Dioryctria abietivorella (Grote) (6)	14	24	22	0	56	7	0
	Dasineura sp. (3)	<1	3	0	0	0	11	0
Western larch	Strobilomyia laricis Michelsen (2)	100						
Engelman spruce	Strobilomyia neanthracina (Czerny) (2)	54	51 (5)	-	-	66 (34)	46 (36)	53 (47)
	Cydia strobilella (L.) (7)	42	48	-	-	30	49	45
	Megastigmus atedius atedius Walker (5)	2	0	-	-	2	3	1
	Mayetiola carpophaga (Tripp) (3)	1	<1	-	-	1	2	<1
	Dioryctria abietivorella (Grote) (6)	<1	0	-	-	1	<1	<1
White spruce	Strobilomyia neanthracina (Czerny) (2)	67	-	64 (117)	74 (34)	73 (12)	-	-
	Cydia strobilella (L.) (7)	30	-	33	21	22	-	-
	Dioryctria abietivorella (Grote) (6)	2	-	1	4	2	-	-
	Mayetiola carpophaga (Tripp) (3)	1	-	1	<1	2	-	-
	Megastigmus atedius atedius Walker (5)	<1	-	<1	<1	<1	-	-
Black spruce	Strobilomyia neanthracina (Czerny) (2)	75	-	71 (8)	79 (1)	100 (1)	-	-
	Cydia stobilella (L.) (7)	10	-	9	21	0	-	-
	Dioryctria abietivorella (Grote) (6)	10	-	13	0	0	-	-
	Megastigmus atedius atedius Walker (5)	6	-	7	0	0	-	-

Table 2 cont.

Conifer	Insect	Overall	Vancouver	Prince Rupert	Prince George	Cariboo	Kamloops	Nelson
Sitka spruce	Strobilomyia neanthracina (Czerny) (2)	48	35 (12)	53 (33)	-	-	-	-
	Cydia strobilella (L.) (7)	39	39	39	-	-	-	-
	Megastigmus atedius atedius Walker (5)	8	25	2	-	-	-	-
	Dioryctria abietivorella (Grote) (6)	5	0	6	-	-	-	-
	Mayetiola carpophaga (Tripp) (3)	<1	1	<1	-	-	-	-
Lodgepole pine	Conophthorus ponderosae (Hopkins) (1)	33	100 (1)	0	0	0	0	0
	Dioryctria spp. (6)	33	0	50 (2)	0	0	0	0
	Eucosma recissoriana Heinrich (7)	33	0	50	0	0	0	0
Western white pine	Conophthorus ponderosa (Hopkins) (1)	67	0	-	-	-	0	67 (3)
	Dioryctria spp. (6)	33	0	-	-	-	0	33
Ponderosa pine	Cydia piperana Kearfott (7)	58	-	-	-	-	60 (10)	50 (2)
	Dioryctria auranticella (Grote) (6)	42	-	-	-	-	40	50
Douglas-fir	Barbara colfaxiana Kearfott (7)	49	30 (129)	56 (7)	0	55 (44)	75 (85)	47 (49)
	Contarinia oregonensis Foote (3)	21	44	5	42	3	4	9
	Dioryctria abietivorella (Grote) (6)	16	9	17	33	32	15	20
	Megastigmus spermotrophus Wachtl. (5)	13	16	21	25	8	5	24
	Choristoneura occidentalis Freeman (7)	<1	<1	0	0	2	<1	0
Western redcedar	Mayetiola thujae (3)	89	88 (8)	0	100 (1)	-	0	0
	seed midge (3)	11	13	0	0	-	0	0
Western hemlock	Megastigmus tsugae (5)	80	100 (2)	67 (3)	0	-	-	0
	Dioryctria abietivorella (Grote) (6)	20	0	33	0	-	-	0
Mountain hemlock	Earomyia sp. (4)	75	87 (3)	54 (4)	-	-	-	0
	scale midge (3)	25	12	46	-	-	-	0
	seed midge (3)	<1	<1	0	-	-	-	0

(1) Coleoptera: Scolytidae
(2) Diptera: Anthomyiidae
(3) Diptera: Cecidomyiidae
(4) Diptera: Lonchaeidae
(5) Hymenoptera: Torymidae
(6) Lepidoptera: Pyralidae
(7) Lepidoptera: Tortricidae

importance, the most damaging insects on conifers suffering frequent heavy seed losses were Dasineura spp. (gall and seed midges) (Diptera: Cecidomyiidae), Earomyia spp. (Diptera: Lonchaeidae) and Megastigmus spp. (Hymenoptera: Torymidae) on true firs; Strobilomyia neanthracina Michelsen (Diptera: Anthomyiidae), and Cydia strobilella (L.) (Lepidoptera: Tortricidae) on all spruces; and Barbara colfaxiana (Kearfott) (Lepidoptera: Tortricidae), Contarinia oregonensis (Diptera: Cecidomyiidae) Foote, Dioryctria spp. (Lepidoptera: Pyralidae) and Megastigmus spermotrophus Wachtl (Hymenoptera: Torymidae) on Douglas-fir.

There appeared to be some geographic variation in damage caused by individual species (Table 2). Of these variations and considering sample sizes, the most notable are for Dasineura abiesema Foote, Megastigmus lasiocarpae Crosby and Dioryctria abietivorella (Grote) on alpine fir; Megastigmus atedius Walker on Sitka spruce; and B. colfaxiana, C. oregonensis, M. spermotrophus and D. abietivorella on Douglas-fir. It is difficult to interpret these differences because of the general and sporadic nature of the collections. Differences in distribution could be due to variations among sites in climatic conditions, stand type, etc. Stand parameters were not recorded for collection sites during the survey.

Not all insects found during the survey are listed in Table 2. Species not listed were those which were only occasionally or rarely found damaging seeds or those whose damage is difficult to identify. An example of the latter group is the western conifer seed bug, Leptoglossus occidentalis Heidemann (Hemiptera: Coreidae). This bug is very common in warm, dry areas, notably were Douglas-fir and pines grow together, and is capable of doing considerable damage. Common cone insects not mentioned are certain scale midges, notably Contarinia washingtonensis Johnson on Douglas-fir and Resseliella sp. (Diptera: Cecidomyiidae) on firs and spruces, and the spruce cone axis midge, Dasineura rachiphaga Tripp (Diptera: Cecidomyiidae) on spruces because these species only occasionally consume seeds. Other species are not listed because their occurrences were rare.

The insects which were the most important relatively were not necessarily those with the greatest potential for damaging individual cone and seed crops. For example, on white and Engelmann spruces S. neanthracina was the most damaging insect (Table 2), but C. strobilella destroyed the largest numbers of seeds at specific sites (Table 3, maximum values). Similarly, the cone maggots Earomyia spp. were most frequently the most damaging pest on grand fir seed (Table 2) but the gall and seed midges, Dasineura spp., were both more damaging to individual crops (Table 3).

Discussion

Knowledge of the historical pattern of seed losses to insects and of the insect complexes affecting seed production by conifers is important, particularly when breeding programs and seed orchards are being planned or when pest management systems are being developed for operational use. The survey results indicate that significant insect problems are not likely to occur in operational seed production of the hemlocks or lodgepole pine. If

Table 3. Seed losses to the most damaging pests in conifers in British Columbia that suffer at least occasional heavy losses

Conifer	Insect	Seeds/half cone slice	
		Avg.	Site max.
Pacific silver fir	Dasineura abiesemia	1.5	6.3
	Dasineura sp. (gall midge)	1.3	8.2
	Earomyia abietum	1.2	18.1
	Barbara sp.	0.6	5.5
	Megastigmus lasiocarpae	0.6	2.3
Grand fir	Dasineura sp. (gall midge)	4.7	33.4
	Dasineura abiesemia	1.6	9.8
	Earomyia abietum & Earomyia sp.	1.2	4.6
	Barbara sp.	0.8	3.0
	Megastigmus pinus & M. rafni	0.3	1.5
	Dioryctria spp.	0.2	1.6
Alpine fir	Earomyia aquilonia	1.4	25.5
	Dasineura abiesemia	0.9	16.7
	Megastigmus lasiocarpae	0.2	3.2
Western larch	Strobilomyia laricis	0.6	3.2
Engelman spruce	Cydia strobilella	2.3	19.7
	Strobilomyia neanthracina	1.5	9.2
	Megastigmus atedius	0.1	3.0
White spruce	Strobilomyia neanthracina	2.3	8.9
	Cydia strobilella	1.3	15.3
Black spruce	Strobilomyia neanthracina	0.7	7.2
	Cydia strobilella	0.2	2.9
Lodgepole pine	Dioryctria spp.	0.8	12.4
	Eucosma rescissoriana	0.7	3.9
Western white pine	Dioryctria spp.	1.9	13.0
	Conophthorus ponderosae	0.8	3.9
Ponderosa pine	Cydia piperana	1.4	4.4
	Dioryctria auranticella	1.1	6.2
Douglas-fir	Barabara colfaxiana	1.4	20.0
	Contarinia oregonensis	0.5	12.4
	Dioryctria spp.	0.4	6.6
	Megastigmus spermotrophus	0.1	1.3
Western redcedar	Mayetiola thujae	0.3	2.0
	seed midge	0.1	1.5

seed orchards were located near forest stands, significant problems are anticipated for true firs, spruces, Douglas-fir and ponderosa pine. In Sitka spruce, western redcedar, western larch and western white pine we anticipate generally light, but with occasional heavy, seed losses.

Even in those conifers which suffer frequent heavy losses, many crops are lightly attacked. The dramatic variability in insect damage emphasizes the need for monitoring systems in situations where application of pest controls are being considered.

Because of the way the data were collected, care must be taken in interpreting the seed production and loss data. For the reasons following, the seed counts per cone slice reported have limited value. However, the data are useful to indicate the conifers for which problems can be anticipated and the relative importance of individual insect species within a complex.

Whole-cone counts are related to slice counts in many conifers (U.S.D.A. 1974). Rudinsky (1955) and DeMars (1964) were among the first to report the use of this method for indexing cone and seed insect damage, specifically for Douglas-fir. A current investigation to quantify the relationship between whole-cone and slice counts for most commercially important conifers in B.C. has revealed that a reasonably good relationship exists for damage caused by most, but not all, cone and seed insects (Author unpubl.). Damage by gall midges, other than the Douglas-fir cone gall midge, and gall adelgids in particular are not indexed well by cone slicing. The relative importance of these insects is underestimated by the cone slice method.

A possible confounding factor is variability in the within-crown distribution of cone and seed insects. For example, damage by C. oregonensis is higher in the upper crown than in the lower crown (Kozak 1963). Thus, damage by this insect would be under-estimated when sampling only the lower crown. However, even though statistically significant differences occurred among crown levels, the differences were not large so the importance of crown level should not be a major concern. Damage by several insects appears to be uniform throughout tree crowns (Kozak 1963) and therefore distribution of samples within crown levels should not be a factor for these species.

Because mature cones were collected during the survey, losses caused by insects which cause mortality of developing conelets are underestimated. Notable insects in this group are Dioryctria spp., Choristoneura occidentalis Freeman (Lepidoptera: Tortricidae) and Conophthorus ponderosae (Hopkins) (Coleoptera: Scolytidae).

The survey results confirm, with a much larger sample size, the relative importance of many insect species. Previous reports have indicated that the more important pests were S. neanthracina and C. strobilella on spruces (Hedlin 1973); C. oregonensis and B. colfaxiana on Douglas-fir (Hedlin 1960, 1961, 1964a; Miller et al. 1984); Earomyia abietum, Megastigmus spp., and seed and gall midges, Dasineura spp., on grand fir (Hedlin 1967b); Mayetiola thujae (Diptera: Cecidomyiidae) on western redcedar (Hedlin 1964b); and Cydia piperana on ponderosa pine (Hedlin 1967a).

With respect to pests on Douglas-fir, Hedlin (1974) and Hedlin et al. (1980) indicated that B. colfaxiana was the major problem in the dry, interior of British Columbia whereas C. oregonensis was the major problem in wet coastal areas. The survey results indicated that this statement on distribution of importance needed some modification. C. oregonensis is the most importance pest on wet sites regardless of whether the site is on the coast or in the interior, as indicated by the relative importance of this species in the Prince George Forest Region as well as at wet sites in other regions. Similarly, B. colfaxiana is the dominant species on warm, dry sites wherever these occur.

Seed losses to insects in other conifers have not been previously quantified for B.C. In addition, several undescribed species have been discovered, notably new species of Dasineura, Earomyia, Cydia, Barbara and an eurytomid. Hopefully, these species will be described in the near future.

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References

DeMars, C.J. 1964. Predicting insect caused damage to Douglas-fir seed from samples of young cones. U.S.D.A. For. Serv. Res. Note PSW-40.

Hedlin, A.F. 1960. On the life history of the Douglas-fir cone moth, Barbara colfaxiana (Kft.) (Lepidoptera: Olethreutidae), and one of its parasites, Glypta evetriae Cush. (Hymenoptera: Ichneumonidae). Can. Ent. 92: 826-834.

Hedlin, A.F. 1961. The life history and habits of a midge, Contarinia oregonensis Foote (Diptera: Cecidomyiidae) in Douglas-fir cones. Can. Ent. 93: 952-967.

Hedlin, A.F. 1964a. Results of a six-year plot study on Douglas-fir cone insect population fluctuation. For. Sci. 10: 124-128.

Hedlin, A.F. 1964b. Life history and habits of a midge, Phytophaga thujae Hedlin (Diptera: Cecidomyiidae) in western red cedar cones. Can. Ent. 96: 950-957.

Hedlin, A.F. 1967a. The pine seedworm, Laspeyresia piperana (Lepidoptera: Olethreutidae), in cones of ponderosa pine. Can. Ent. 99: 264-267.

Hedlin, A.F. 1967b. Cone insects of grand fir, Abies grandis (Douglas) Lindley, in British Columbia. J. Entomol. Soc. B.C. 64: 40-44.

Hedlin, A.F. 1973. Spruce cone insects in British Columbia and their control. Can. Ent. 105: 113-122.

Hedlin, A.F. 1974. Cone and seed insects of British Columbia. Can. For. Serv., Pacific Forestry Centre, Victoria, B.C., Info. Rept. BC-X-90.

Hedlin, A.F., H.O. Yates III, D. Cibrian Tovar, B.H. Ebel, T.W. Koerber and E.P. Merkel. 1980. Cone and seed insects of North American conifers. Can. For. Serv./U.S.D.A. For. Serv./Sec. Agric. Recur. Hidraul., Mexico. Victoria, B.C. 122 p.

Kozak, A. 1963. Analysis of some factors associated with distribution and intensity of attack by cone and seed insects in Douglas-fir. University of British Columbia, Faculty of Forestry, Ph.D. Thesis, 179 p.

Miller, G.E., A.F. Hedlin and D.S. Ruth. 1984. Damage by two Douglas-fir cone and seed insects: correlation with cone crop size. J. Entomol. Soc. B.C. 81: 46-50.

Rudinsky, J.A. 1955. Douglas-fir cone and seed insects (progress report). Weyerhaeuser For. Res. Note No. 13.

U.S.D.A. Forest Service. 1974. Seeds of woody plants in the United States. U.S. Department of Agriculture Handbook 450, Washington, D.C. 883 p.

Winjum, J.K., and N.E. Johnson. 1960. A modified knife-cone cutter for Douglas-fir seed studies. J. For. 58: 487-488.

THE CONE AND SEED INSECTS OF TAMARACK IN EASTERN NORTH AMERICA

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ABSTRACT

The complex of insects causing damage to the cones and seeds of tamarack (Larix laricina (Du Roi) K. Koch) in New Brunswick and Maine are reviewed and their biology, habits, distribution, and damage are discussed. Two species, Lasiomma viarium (Huckett) and the spruce budworm, Choristoneura fumiferana (Clemens) are considered of primary importance. A Resseliella sp. and a Megastigmus sp. appear to be of secondary importance, while several other insects are occasional feeders on tamarack cones and seeds. Damage levels were highly variable, but ranged up to 88.0 % of the seed crop.

INTRODUCTION

Tamarack (Larix laricina (Du Roi) K. Koch) is a small to medium sized tree with a transcontinental distribution in boreal North America. Despite its fast growth compared to other commercially important coniferous species in the Boreal Forest Region (Mead, 1978; Hall, 1983) and the Acadian Forest Region (MacGillivray, 1969) it has been largely ignored as a reforestation species. More recently, increasing interest has been shown in tamarack as a reforestation species and the New Brunswick Tree Improvement Council has begun a breeding program to improve the species (Simpson, 1983).

Prior to 1982 relatively little was known about the insects of tamarack cones and seeds. It had been noted that seed production was unreliable (Simpson, 1983; Smith, 1981) and some damage-causing insects had been isolated from tamarack cones (Hedlin et al., 1981; Kettela and Brown, 1968; Marcovitch, 1914; McAlpine, 1956; and Rose and Lindquist, 1980). No studies had investigated the insect fauna associated with the cones of tamarack until 1982 when investigations were initiated at the Universities of New Brunswick (Amirault, 1984; Brown and Amirault, 1985; Amirault and Brown, 1986) and Maine (Eavy and Houseweart, 1986; Eavy, 1987). This paper reviews all known information on the cone and seed insects of tamarack including the biology, habits, distribution, and damage caused by these insects.

BIOLOGY, HABITS, AND DISTRIBUTION

Lasiomma spp.(Diptera: Anthomyiidae)

In both New Brunswick (Amirault and Brown, 1986) and Maine (Eavy, 1987) Lasiomma spp. were found to be the most damaging insects associated with the cones of tamarack. Lasiomma viarium (Huckett) was identified from both areas and a Lasiomma n. sp. nr. laricicola (Karl) was reported from Maine. Oviposition occurred during the first two or three weeks in May. Eggs were laid singly between the scales, usually in the lower half of cones. Larvae were active in the cones from late May until early July (Figure 1). They fed upwards in a spiral pattern around the cone axis, burrowing through the lower portions of the scales and the seeds. Mature larvae left the cones from mid-June to mid-July. In New Brunswick they were observed leaving during wet weather. They dropped to the ground and formed puparia, in which they remained until the following May. Most seeds damaged by the cone maggot were in the basal half of the cone. The holotype of this species was collected near Churchill, Manitoba (Huckett, 1965) indicating that it may occur throughout the eastern portion of the range of tamarack.

Three species of Lasiomma were associated with tamarack studied by Hedlin et al., 1981. Lasiomma anthracina (Czerny) is a major pest of spruce (Picea sp.) cones, and was suggested to also occur on tamarack. L. laricicola (Karl) and L. carbonarium (Ringdahl) were reared from tamarack cones collected in Alberta and Manitoba respectively.

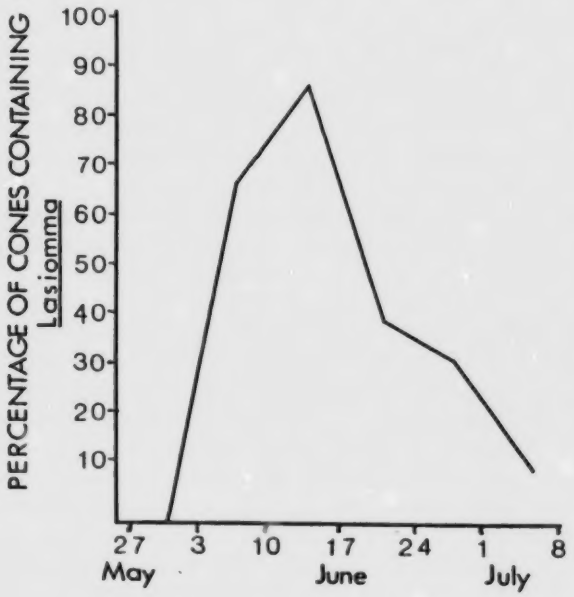

Figure 1. Frequency of L. viarium larvae found within tamarack cones collected from a 20-year-old stand in central New Brunswick (from Amirault and Brown, 1986).

Choristoneura fumiferana (Clemens) (Lepidoptera: Tortricidae)

The second most damaging pest of tamarack cones in New Brunswick was the spruce budworm (Amirault and Brown, 1986), while in Maine, it was not identified as a major factor by Eavy (1987). It fed on the cones at about the same time of year as L. viarium. The budworm larvae displayed two different feeding habits depending on their stage of development. In early May second-instar larvae burrowed into the developing cones and fed inside. From late May or early June to early July, older larvae fed externally on cones, often completely destroying them. There was an apparent preference for cones over foliage as a food source. The range of the spruce budworm (Harvey, 1985) approximates that of tamarack.

Resseliella sp. (Diptera: Cecidomyiidae)

The most common insects within tamarack cones were larvae of a Resseliella sp. (Eavy (1987) reported R. conicola). In Maine, up to 45 and in New Brunswick up to 30 larvae per cone were recorded. In both areas this species was considered a primary predator of seed, not just a scavenger. Adults of a Resseliella sp. were collected in traps in early June as they emerged, and in mid-June larvae were first observed within cones. In late July and early August, mature larvae (3.5mm in length and orange) left the cones to overwinter on the ground.

Megastigmus sp. (Hymenoptera: Torymidae)

A Megastigmus sp. (probably laricis (Marcovitch)) was found in seed from Maine and New Brunswick. Oviposition occurred near the end of May. Larvae developed in the seeds, completely hollowing them by the end of the summer. The holotype of M. laricis was collected at Ithaca, New York (Marcovitch, 1914).

Earomyia aquilonia McAlpine (Diptera: Lonchaeidae)

The fly, Earomyia aquilonia, was reared from tamarack cones collected in Alberta (McAlpine, 1956), and had also been collected in British Columbia (Keen, 1958). The distribution of E. aquilonia (Hedlin et al., 1981) approximates that of tamarack. It was not reported in either the Maine or New Brunswick studies.

Other Lepidoptera

Lepidoptera of minor importance were Spilonota ocellena, Heinemann (Olethreutidae), Zeiraphera improbana, Walker (Tortricidae), and Coleotechnites laricis Freeman (Gelechidae) which were noted as early season cone miners (Amirault and Brown, 1986; Eavy, 1987). Other Lepidoptera observed to be occasional feeders on tamarack cones were Choristoneura rosaceana Harris (Tortricidae), Hypagytris piniata Packard (Geometridae), and Holcocera immaculella (McDunnough) (Blastobasidae) (Amirault and Brown, 1986).

DAMAGE CAUSED BY TAMARACK CONE AND SEED INSECTS

The main study area in New Brunswick was a 20-year-old stand in which moderate to heavy cone crops occurred throughout the study period. Estimates of seed damaged by insects in this stand were 88.0% in 1982, 74.2% in 1983, and 73.5% in 1984. These estimates were computed by averaging the percentages of damaged seed in weekly collections made in July and August. In a 7-year-old stand the amount of damaged seed dropped from 74.0% in 1982 to 24.6% in 1983. This stand had not borne cones prior to 1981 when a small number were produced, and produced a light crop and a heavy crop in 1982 and 1983, respectively. No Megastigmus sp. were found in this stand, suggesting that several seasons following the onset of cone production may be required before a full complement of the cone and seed insect fauna become established.

Seasonal damage trends (Figure 2) show a sharp increase in June. This was a result of the combined feeding effects of L. viarium and the spruce budworm. Relatively little additional damage was recorded after June.

Eavy (1987) reported much lower levels of damage in Maine than were found in New Brunswick (Table 1). This was in spite of a pilot study that found damage to tamarack seed ranged from 55-73% by late July, and a statewide survey that showed over 80% of the seed to be damaged by mid-August. Eavy (1987) considered L. viarium to be a more important predator of seeds than the Lepidoptera. Eavy and Houseweart (1986) noted that 30-60% of the seed from their study areas was innately inviable. Similiar figures were obtained in New Brunswick from seed not damaged by insects.

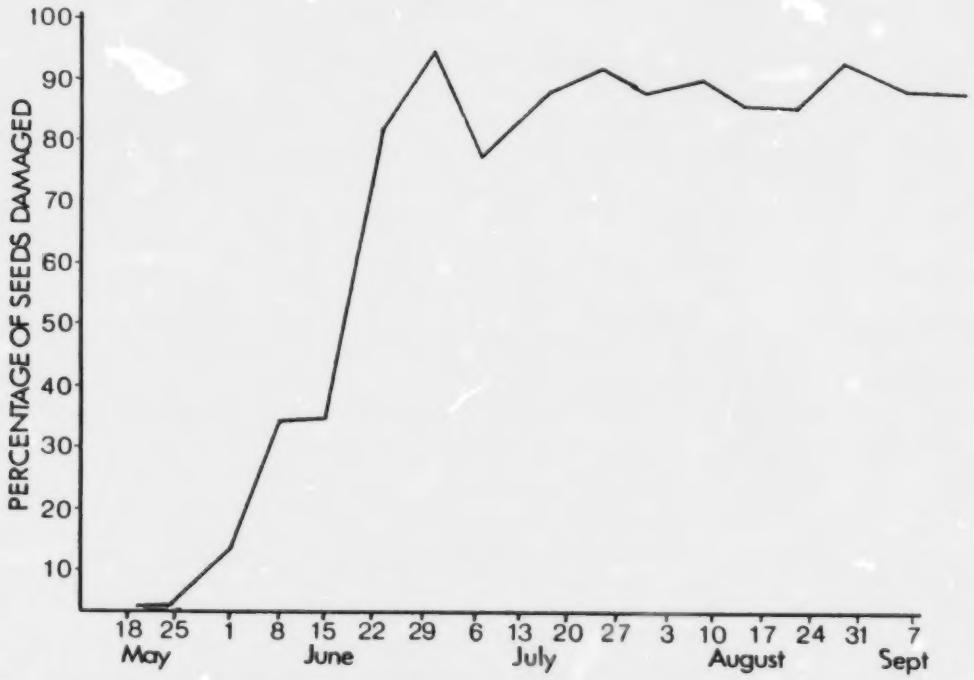

Figure 2. Percentages of tamarack seeds damaged by cone and seed insects in a 20-year-old stand in New Brunswick, 1982 (estimates derived from weekly collections).

Table 1. Estimated percentages of tamarack seed crop destroyed by various insect species.

	Maine[1] 1982-84	New Brunswick[2] (20-year-old stand) 1983	1984
Lasiomma spp.	6.0	29.0	38.6
Spruce Budworm	7.0[3]	28.7	5.7
Other Lepidoptera		8.2	1.9
Resseliella sp.	3.0	5.9	17.1
Megastigmus sp.	0.1	2.4	10.2

[1] Eavy, 1987
[2] Brown and Amirault, 1985; Amirault and Brown, 1986
[3] All Lepidoptera including spruce budworm

The breakdown of damage by causal agent in the 20-year-old stand showed an interesting trend between 1983 and 1984 (Table 1). Spruce budworm damage was quite variable depending on the population density within the stand. A large reduction in budworm damage in 1984 was offset by increased damage by other insects. The total amount of damage remained virtually unchanged, indicating that there is competition for the resource between various insect species. This implies that control strategies developed for tamarack cone and seed insects will have to be flexable, or seperate strategies developed to deal with different insects at various times.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Amirault, P.A. 1984. An investigation of the cone and seed insects of eastern larch, Larix laricina (Du Roi) K. Koch, and attempts to control damage using chemical insecticides. Unpubl. M. Sc. For. Thesis, Univ. of New Brunswick. 63 p.

Amirault, P.A. and N. Rae Brown. 1986. Cone and seed insects of tamarack Larix laricina (Du Roi) K. Koch, and attempts to control damage using chemical insecticides. Can. Ent. 118: 589-596.

Brown, N. Rae and P.A. Amirault. 1985. Studies on the biology and control of cone and seed insects of selected conifers in the Maritime Provinces. Unpubl. Contract Report Submitted to the Canadian Forestry Service, Maritimes.

Eavy, A.L. and M.R. Houseweart. 1986. Larch seed and cone insects. In Anonymous. 1986. 1986 larch workshop. Joint Publ. Can. For. Serv., N.B. Dept. Nat. Res. Energy. 170 p.

Eavy, A.L. 1987. Cone and seed mortality factor distribution in two natural populations of tamarack in central Maine. Unpubl. PhD. For. Res. Thesis, Univ. of Maine. 100p.

Hall, P.J. 1983. Comparison of the growth of larch and other conifers on reforested and afforested sites in Newfoundland. For. Chron. 59(1): 14-16.

Harvey, G.T. 1985. The taxonomy of the coniferophagus Choristoneura (Lepidoptera: Tortricidae): A review. In Sanders, C.J., R.W. Stark, E.J. Mullins, and J. Murphy. 1985. Recent advances in spruce budworms research. Proc. of the CANUSA Spruce Budworms Res. Sym., Can. For. Serv., U.S. Dept. Agr. For. Serv. 527 p.

Hedlin, A.F., H.O. Yates III, D.C. Tovar, B.H. Ebel, T.W. Koerber, and E.P. Merkel. 1981. Cone and seed insects of North American conifers. Can. For. Serv., U.S. Dep. Agric. For. Serv., Secretaria de Agricultura y Resources Hidraulicos, Mexico. 122 p.

Huckett, H.C. 1965. The Muscidae of northern Canada, Alaska, and Greenland (Diptera). Mem. Entomol. Soc. Can. 42, 369 p.

Keen, F.P. 1958. Cone and seed insects of western forest trees. U.S. Dept. Agric. For. Serv., Tech. Bull. 1169, 168 p.

Kettela, E.G. and N. Rae Brown. 1968. A note on the occurrence of Adelges strobilobius (Homoptera: Adelgidae) in cones of eastern larch. Can. Ent. 100(8): 894.

Marcovitch, S. 1914. A species of Megastigmus reared from larch seeds. Can. Ent. 46(12): 435-438.

MacGillivray, H.G. 1969. Larches for reforestation and tree improvement in eastern Canada. For. Chron. 45(6): 440-444.

McAlpine, J.F. 1956. Cone-infesting lonchaeids of the genus Earomyia Zett; with descriptions of five new species from western North America (Diptera: Lonchaeidae). Can. Ent. 88(4): 178-196.

Mead, D.A. 1978. Comparative height growth of eastern larch and black spruce in northwestern Ontario. For. Chron. 54(6): 296-297.

Rose, A.H. and O.H. Lindquist. 1980. Insects of eastern larch, cedar, and juniper. Dept. Environ., Can. For. Serv., For. Tech. Rept. 28, 99 p.

Smith, R.F. 1981. How early can tamarack cones be collected? Can. For. Serv., Maritimes For. Res. Cen., Tech. Note 35. 6p.

Simpson, J.D. 1983. The New Brunswick tree improvement council's breeding strategy for tamarack. pp. 219-224 in Proceedings 28th Northeastern Forest Tree Improvement Conference, Univ. New Hampshire, 7-9 June, 1982, Durham.

REVIEW OF INSECTS FOUND IN CONES OF ABIES ALBA MILL IN POLAND[1]

by

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SUMMARY

The results of the studies on the entomofauna of cones of Abies alba Mill. conducted in southern Poland during 1976-1986 are summarized in this paper. The cone samples were collected in the forests of the Sacz Beskid and the Ojców, Tatra, and Roztocze National Parks. A total of 45 insect species from the following 6 orders were found: Heteroptera (2 species), Coleoptera (12), Raphidioptera (1). Hymenoptera (16), Lepidoptera (2) and Diptera (12). The following coenotic groups were distinguished:

- conophagous insects: 3 species (Barbara herrichiana Obr., Dioryctria abietella (Den. et Schiff.) and Earomyia impossibile Morge);

- seminiphagous insects: 2 species (Megastigmus suspectus Borr. and Resseliella piceae Seitn.);

- parasitoids of the two insect groups mentioned above: 17 species;

- saprophagous and coprophagous insects: 8 species;

- seasonal insects: 15 species.

Connections between parasitoids and their hosts were established: Macrocentrus collaris Spin. - host Barbara herrichiana Obr.; Mesopolobus pinus Hussey - host Megastigmus suspectus Borr.; Platygaster sp. near manto Walk. - host Resseliella piceae Seitn. The vertical distribution range has been given. A largest number of species, viz. 26 occurred in the material from the Roztocze National Park, which is situated at the north-eastern boundary of the fir's natural range. The studies on the cone insects of fir should be continued not only for the scientific but also for the economic reason.

Keywords: cone and seed insects, coenotic groups, fir.

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[1] Worked out on the basis of studies concerning problems R-II-9, MR.II.18 and no contract basis topic.

RESUME

La révision des insectes trouvés dans les cones du sapin Abies alba Mill. dans le Sud de la Pologne. Dans cet ouvrage, ou a montre les resultats des recherches de entomofaune des cônes de sapin, faites en Pologne, dens les années 1976-1986.

Les énchantillons des sapins one éte ramasés dans la montagne de Beskid Sadecki, et dans les parcs nationals: le Parc de Ojcóv, le Parc de Tatra et le Parc de Roztocze. Ou y a trouvé 45 espèces des insectes appartenant toutes à 6 ordres différents: Heteroptera (2 espèces), Coleoptera (12), Raphidioptera (1), Hymenoptera (16), Lepidoptera (2) et Diptera (12).

Les groupes cénotiques suivants ont été dégagés:

- insectes conophages: 3 espèces (Barbara herrichiana Obr., Dioryctria abietella (Den. et Schiff.) et Earomyia impossibile Morge);
- insectes seminiphages: 2 espèces (Megastigmus suspectus Borr. et Resseliella piceae Seitn.);
- insectes parasites des 2 groupes précédents: 17 espèces;
- insectes saprophages et coprophages: 8 espèces;
- insectes saisonniers: 15 espèces.

On a fait des liasions entre les parasites et les hôtes. Macrocentrus collaris Spin. est le parasite de Barbara herrichiana Obr.; Mesopolobus pinus Hussey est le parasite de Megastigmus suspectus Borr.; Platygaster sp. aff. manto Walk. est le parasite de Resseliella piceae Seitn. Ou a montre le limite vertical de ces insectes. Relativement, la plupart des insectes on a trouvédans le Parc de Roztocze, ou est la limite du zône des sapins.

Il est souhaitable de poursuivre les recherches en prennant en consideration un aspect economique et scientifique: dans cette population des insectes il y a des ravageurs des graines.

Mots-clefs: insectes ravageurs, cônes, graines, groupe cénotique, sapin.

INTRODUCTION AND METHODS OF INVESTIGATION

The mortality of Abies alba Mill. has considerably increased in Europe during the last several decades. The basic and most proper form of regeneration of this species is natural seeding which is affected by many limiting factors. Among them the insects damaging seeds and cones play an important role (Skrzypcynska 1982).

The field and laboratory studies on the entomofauna of cones of Abies alba Mill. were conducted during 1976-1986. The cone samples were collected in numerous localities in five regions[2] of Southern Poland, namely in the Piwniczna Management Unit (1) and the Krynica Experimental Forest (2), both situated in the Sacz Beskid, and also in the Ojców (3), Tatra (4), and Roztocze National parks (5) (Fig. 1).

The cones were collected from randomly selected fir trees growing at the elevation from 260 to 1200 m a.s.l. on the following site types of forest: mixed mountain forest, riparian mountain forest, and montain forest. The insect adults were obtained through individual (1 cone in a glass jar) and mass rearing from ripening and ripe cones and also from seeds. The larvae and pupae were obtained through analyses of cones and seeds. The methods have been already presented in detail in earlier work (Skrzypczynska 1981).

RESULTS

A total of 45 insect species were found in the cones analyzed. They belonged to the following 6 orders: Heteroptera (4.4% of all species obtained), Coleoptera (26.7%), Raphidioptera (2.2%), Hymenoptera (35.6%), Lepidoptera (4.4%) and Diptera (26.7%) (Fig. 2). A largest number of species, viz. 26 occurred in the material from the Roztocze National park, which is situated at the north-eastern boundary, of the fir's natural range (Skrzypczyńska et al. 1987).

The following coenotic groups were distinguished on the basis of the trophic connections of the insects living in fir's cones and seeds:

I. Conophagous insects - their larvae while feeding, devastate the seed scales of cones together with the seeds inside;

II. Seminiphagous insects - their larvae feed inside seeds;

III. Parasitoids and predators of conophagous and seminiphagous insects;

IV. Saprophagous and coprophagous insects - their larvae feed on dead organic substance (e.g., imperfect seeds) and on excrements of caterpillars infesting the cones;

V. Seasonal insects for which the cone has provided shelter, frequently unexpected (Table 1).

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[2] See Table 1

Table 1. List of insects obtained from cones of Abies alba Mill. in Poland during 1976-1986.

No.	Order, family, species	Coenotic group	Region[1]	Altitude (m)
1	2	3	4	5
	HETEROPTERA: Miridae			
1.	Poeciloscytus sp.	V	5	260-390
	Tringitidae			
2.	Stephantis sp.	V	5	260-390
	COLEOPTERA: Rhizophagidae			
3.	Rhizophagus dispar (Payk.)	V	2	650
	Mycetophagidae			
4.	Typhaea stercorea (L.)	V	4	900-1000
	Cryptophagidae			
5.	Cryptophagus (Micrambe) abietis (Payk.)	V	1,2,3,4	500-1010
6.	Cryptophagus subdepressus Gyllh.	V	4	900-1000
7.	Cryptophagus subfumatus Kr.	V	4	900-1010
8.	Cryptophagus sp.	V	4	900-1000
	Lathridiidae			
9.	Cartodere elongata Curt.	V	4	900-1000
10.	Cartodere filum (Aubé)	V	1,5	260-840
11.	Corticaria fulva (Comolli)	V	1	600
12.	Enicmus minutus (L.)	V	2,5	260-600
13.	Lathridius nodifer Westw.	V	4	900-1000
	Endomychidae			
14.	Mycetaea hirta (Marsh.)	V	4	900-1000
	RAPHIDIOPTERA: Raphidiidae			
15.	Rhaphidia ophiopsis Schumm.	III	5	260-390
	HYMENOPTERA: Ichneumonidae			
16.	Townesia tenuiventris Holmgr.	III	5	260-390

Table 1. (Continued)

No.	Order, family, species	Coenotic group	Region[1]	Altitude (m)
1	2	3	4	5
17.	Mesostenus albinotatus Grav.	III	5	260-390
18.	Mesostenus transfuga Grav.	III	5	260-390
19.	Mesostenus sp.	III	5	260-390
20.	Venturia sp.	III	5	260-390
	Braconidae			
21.	Apanteles sp.	III	5	260-390
22.	Aphaereta tenuicornis Nix.	III	5	260-390
23.	Bracon sp.	III	2	600
24.	Glabrobracon variator Ns.	III	5	260-390
25.	Macrocentrus collaris Spin.	III	1	600
	Embolemidae			
26.	Embolemus antennalis Kieff.	V	5	260-390
	Pteromalidae			
27.	Anogmus piceae (Ruschka)	III	2	720
28.	Mesopolobus pinus Hussey	III	5	260-390
29.	Pteromalus sp.	III	2	580-600
	Torymidae			
30.	Megastigmus suspectus Borries	II	1,2,3,4,5	260-1010
	Platygastridae			
31.	Platygaster sp. near manto Walk.	III	1	640-800
	LEPIDOPTERA: Tortricidae			
32.	Barbara herrichiana Obr.	I	1,2,5	260-860
	Pyralidae			
33.	Dioryctria abietella (Den. et Schiff.)	I	1,2,3,4,5	260-1030
	DIPTERA: Sciaridae			
34.	Lycoriella cellaris (Leng.)	IV	1,2,3,4	400-1200
35.	Lycoriella solani Winn.	IV	4,5	260-1200
	Cecidomyiidae			

Table 1. (Continued)

No.	Order, family, species	Coenotic group	Region[1]	Altitude (m)
1	2	3	4	5
36.	Asynapta strobi (Kieff.)	IV	2	620-800
37.	Camptomyia sp.	IV	1,2,3,4,5	260-1030
38.	Clinodiplosis cilicrus (Kieff.)	IV	5	260-390
39.	Lestodiplosis ?holstei Kieff.	III	1,2,3,5	260-840
40.	Resseliella piceae Seitn. Lonchaeidae	II	1,2,3,4,5	260-1200
41.	Earomyia impossibile Morge Heleomyzidae	I	1,2,3,4,5	260-1200
42.	Tephrochlamys flavices Zett. Chloropidae	IV	2	600
43.	Hapleginella laevifrons (Loew) Drosophilidae	IV	2,5	260-710
44.	Drosophila repleta Wollast Larvaevoridae	IV	1,2	700-710
45.	Actia nudibasis Stein.	III	5	260-390

[1] Explanation in text.

Barbara herrichiana Obr., Dioryctria abietella (Den. et Schiff.) and Earomyia impossibile Morge[3] belonged to group I, while Megastigmus suspectus Borr. and Resseliella piceae Seitn. to group II. As far as group III is concerned there were 17 species found, out of which Mesopolobus pinus Hussey is a parasitoid of larvae of M. suspectus, and Macrocentrus collaris Spin. turned out to be a parasitoid of B. herrichiana. The larvae of R. piceae were hosts to the larvae of Platygaster sp. near manto Walk.[4] while Actia nudibasis Stein. was a parasitoid of D. abietella. Townesia tenuiventris Holmgr. turned out to be a possible parasitoid of D. abietella, while Anogmus piceae (Ruschka) - a possible parasitoid of R. piceae. The remaining parasitoids listed in table 1 were obtained from mass rearings, not from individual rearings, and this is why it was difficult to establish a direct connection in a system parasitoid - host.

The following 8 species belonged to the group of saprophagous and coprophagous insects: Lycoriella cellaris (Leng.), L. solani Winn., Asynapta strobi Winn., Camptomyia sp., Clinodiplosis cilicrus (Kieff.), Tephrochlamys flavices Zett., Hapleginella laevifrons (Loew) and Drosophila repleta Wollast. The remaining 15 species listed in table 1 were classified as seasonal insects, and their presence in fir's cones was accidental. The cones may have served for example as a shelter.

The vertical distribution of the species found in fir's cones is very interesting. The conophagous insects occurred at various elevations, e.g., B. herrichiana from 260 to 860 m, D. abietella from 260 to 1030 m, and E. impossibile from 260 to 1200 m above sea level. The seminiphagous species M. suspectus and R. piceae inhabited cones of fir trees growing at the elevations of 260-1010 m a.s.l. and 260-1200 m a.s.l. respectively. Out of 15 species of parasitoids and predators, 10 species occurred at lower elevation from 260 to 390 m a.s.l., and only Platygaster sp. near manto was found at the elevations from 640 to 800 m a.s.l. Out of predatory insects Lestodiplosis ? holstei Kieff. occurred at various elevations from 260 to 840 m a.s.l. Most of beetles were connected with cones of firs growing at relatively high elevations from 900 to 1000 m, and sometimes 1010 m a.s.l. (Table 1).

DISCUSSION

According to literature there were also some other insect species reported from fir's cones which were not obtained by the author of this paper. For example from the U.S.S.R. such species have been reported as Megastigmus strobilobius Ratz. (Hym., Torymidae) (Prisyazhnyuk 1949), Eupithecia abietaria var. debrumeata St. and E. gigantea St. (Lep., Geometridae), Hyphantidium terebrellum Zinck. (Lep., Pyralidae), Lasiomma abietis Huck. (Dipt., Anthomyiidae), Earomyia grusia Morge (Dipt., Lonchaeidae) (Stadnitzky et al. 1978), and Earomyia viridana (Meig.) (Kozikowski and Kuntze 1936, Morge 1962,

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[3] From the culture was obtained Earomyia ? grusia Morge, det. Prof. Dr. G. Morge, but its determination is problematic because its sexual organs are not fully mature.

[4] I wish to thank Dr. H. Vlug, The Netherlands, for this information.

Kapuscinski 1966). In France, Rogues (1983) reported from fir's cones also Epinotia nigricana H.S. (Lep., Tortricidae), Zeiraphera rufimitrana H.S. (Lep., Tortricidae), Lasiomma abietis Huck. (Dipt., Anthomyiidae) and Earomyia sp. (Dipt., Lonchaeidae).

The world list of insects attacking cones and seeds of first have been presented by Yates (1986).

In conclusion, the studies on the insects inhabiting fir cones should be continued for scientific as well as economic reasons.

LITERATURE CITED

Kapuściński, S., 1966: Szkodniki owadzie nasion drzev leśnych. PWRiL, Warszava, 155 pp.

Kozikowski, A. and R. Kuntze, 1936: Szkodniki nasion jodly wystepujace w poludniowej Polsce. Sylwan, A, vol. 54, pp. 93-112.

Morge, G., 1962: Monographie der palearktischen Lonchaeidae. Beitr. Ent., vol. 12, pp. 381-434.

Prisyazhnyuk, A.A., 1949: Bolezni i vrediteli semian drevesnȳkh i kūstarnikovȳkh porod i merȳ borbȳ s nimi. Vseros. Obshch. Okhr. Prir., Moskva, 63 pp.

Rogues, A., 1983: Les insectes ravageurs des cônes et graines de conifères en France. INRA, Paris, 135 pp.

Skrzypczyńska, M., 1981: The entomofauna of the cones of fir (Abies alba) in Poland. Mitteil, d. Schweizer. Entom. Gesel., vol. 54, pp. 291-295.

Skrzypczyńska, M., 1982: Szkodniki nasion i szyszek jodły pospolitej Abies alba Mill. na wybranych stanowiskach w Beskidzie Sadeckim w latach 1976-1980. Acta Agr. et Silv. ser. Silv. vol. 21, pp. 79-97.

Skrzypczyńska, M., M. Kozioł, F. Dembińska, and B. Wiśniiovski, 1987: Preliminary studies on the entomofauna of cones of Abies alba Mill. in the Roztocze National Park in Poland. Zeit. f. ang. Ent. vol. 104, pp. 39-46.

Stadnitzky, G.V., G.I. Jurchenko, A.N. Smetanin, V.P. Grebenshchikova and M.V. Pribȳlova, 1978: Vrediteli shishek i semian khvoynȳkh porod. Lesnaja promȳshlennost, Moskva, 168 pp.

Yates III, H.O., 1986: Checklist of insect and mite species attacking cones and seeds of world conifers. J. Entomol. Sci. 21, pp. 142-168.

VALUE OF CUTICULAR HYDROCARBONS FOR IDENTIFYING MORPHOLOGICALLY SIMILAR SPECIES OF PINE CONE BEETLES

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SUMMARY

Cuticular hydrocarbons are evaluated as a suite of taxonomic characters for six species of Conophthorus: C. ponderosae, C. radiatae, C. cembroides, C. coniperda, C. resinosa, and C. banksianae. We identified a total of 69 individual and isomeric mixtures of hydrocarbons. Hydrocarbon components consist of n-alkanes, alkenes, alkadienes, 2- or 4-methylalkanes, 3-methylalkanes, single component and isomeric mixtures of internally-branched monomethylalkanes, dimethylalkanes and trimethylalkanes. Hydrocarbon mixtures in three geographically-separated populations of C. ponderosae from three different pine species are qualitatively the same with the exception of a homologous series of 3,7-dimethylalkanes from C. ponderosae collected from Pinus lambertiana. This implies that sibling species may exist in the C. ponderosae complex. Hydrocarbon patterns of C. resinosae and C. banksianae appear to be qualitatively identical; no unique hydrocarbon components were found. This supports the concern that C. banksianae is not a valid species. The results of this preliminary study indicate that cuticular hydrocarbons could be used to separate species of Conophthorus. To be useful as chemotaxonomic characters, hydrocarbons should be abundant, not minor components. They should also be unique or present in only a few of the species, or conversely, they should be common in most of the species, yet completely absent, rare, or of insignificant quantities in one or a few. Furthermore, they should have a unique elution time so that they do not coelute with another hydrocarbon in the same species nor should they elute at a time similar to a different hydrocarbon in a different species. Hydrocarbons which meet these criteria were found in five of the six Conophthorus species.

KEY WORDS--Cuticular lipids, chemotaxonomy, methyl-branched hydrocarbons, mass spectra, Conophthorus species, Pinus species, Scolytidae, insect integument.

INTRODUCTION

Conophthorus Hopkins (family Scolytidae) is a taxonomically refractory genus that is destined to increase in importance as an economic pest as production forestry in northern and western North America becomes more reliant on pine seed orchards. Future pest management strategies for these beetles will rely on control strategies or monitoring techniques based on species-specific behavior of adults. Without proper identification of species or a clear understanding of the interaction between hosts and Conophthorus species, development of a viable pest management program will not be possible.

Adult Conophthorus characteristically attack and kill female cones of Pinus. In severe infestations nearly all of the cones may be destroyed (Furniss and Carolin 1977). Such sizable reductions in seed crops can adversely affect reforestation, whether the stands are naturally regenerated or planted with seedlings. With few exceptions female beetles bore into second-year cones from May to July. One species, C. banksianae McPherson, exclusively infests twig terminals. Other species survive in twigs when cones are not available. Female beetles initiate attack through the cone stalk or through the side of the cone near its base. They rapidly girdle the axis of the cone, thereby severing the conductive tissue and killing the cone. Infested cones remain on the tree or drop to the ground. Larvae mine the cone, complete their development, and overwinter in the same cone. In some species, these brood adults may remain in diapause for an additional year (Williamson et al. 1966; Jenkins 1982).

The genus Conophthorus is restricted to North America. Keys to the species utilize morphological features of the elytra and pronotum (Wood 1982). Wood (1982) notes that "character diversity in this genus is limited. Characters are poorly developed and variable, making the separation of some species extremely difficult." Host species can be used, and in fact are used almost exclusively, to identify beetle species (Hedlin et al. 1980). Most species of Conophthorus are apparently monophagous. C. ponderosae Hopkins is a notable exception to this generalization. This species apparently breeds in 13 species of Pinus and ranges from northern British Columbia to southern Mexico. In a recent revision of the genus, Wood (1982) synonymized C. ponderosae with five other species of Conophthorus: C. scopulorum Hopkins, C. contortae Hopkins, C. monticolae Hopkins, C. flexilis Hopkins, and C. lambertianae Hopkins. He based his revision on the holotypes of all the above species and 784 other specimens. He concluded "...the variability in this material is difficult to interpret. It is entirely possible that two or more sibling species are represented."

During speciation species normally also develop morphological differences which we, as biologists, use to identify them. Some species fail to acquire conspicuous morphological differences during the process of speciation and are called sibling species (Mayr 1969). Sibling species are obviously inconvenient to museum taxonomists, however, they also pose significant problems for forest biologists, including pest management specialists. Correct taxonomic classification is fundamental to understanding all biological processes.

Since the different species of Conophthorus are difficult to separate morphologically, we decided to evaluate cuticular hydrocarbons as another suite of taxonomic characters for species determination. It seems incongruous that only one species of Conophthorus would be polyphagous. It is possible that C. ponderosae is in the process of speciation or that there are true biological (albeit sibling) species awaiting discovery. Our overall goal is to examine the taxonomic status of all species of Conophthorus by evaluating a set of characters other than morphological features. We have chosen to examine the cuticular hydrocarbons as a possible additional set of taxonomic characters.

Insect Hydrocarbons

The surface of all terrestrial insects is covered with a thin layer of wax that increases their fitness (Hadley 1985). This wax plays a key role in survival of the insect by providing protection from dessication (Hadley 1982), as well as serving as a barrier to abrasion, microorganisms, and chemicals (Blomquist and Dillwith 1985; Jackson and Blomquist 1976). Some wax components have been shown to serve a major function in chemical communication as pheromones and kairomones (Howard and Blomquist 1982). Hydrocarbons are the predominant lipids in insect waxes.

Alkanes occur in all the insect surface lipids so far investigated. The n-alkanes generally range from 21 to 36 carbons atoms with alkanes having an odd number of carbons predominating. 2-Methylalkanes and/or 3-methylalkanes are also prevalent in insect surface lipids. Like the n-alkanes, the terminally-branched monomethylalkanes range from simple compositions where only one compound is present to complex mixtures of 2-methylalkanes, 3-methylalkanes or mixtures of 2- and 3-methylalkanes. The 2-methylalkanes are somewhat unique in that components with both odd- and even-numbered carbon chains are present in substantial amounts, which reflects their biosynthetic origin from the carbon skeleton of valine and leucine (Blomquist and Dillwith 1985).

The majority of the internally-branched monomethylalkanes have the methyl branch located on an odd-numbered carbon atom between carbons 5 and 17. Monomethylalkanes with the methyl branch on even-numbered carbon atoms are usually minor components. Many of the long-chain, internally-branched dimethylalkanes have an isoprenoid-type spacing, although they are not derived from isoprenoid units. Common isomers are 9,13-; 11,15-; 13,17-; 15,19- and 17,21-. Methyl branches on many other positions have been reported. As careful analyses of dimethylalkanes are made on more species, it appears that the methyl groups can be positioned almost anywhere on the chain, although usually on odd-numbered carbons. n-Alkenes, with one, two, or three double bonds, have been characterized from about one-half of the insect species examined to date. The chain length of cuticular n-alkenes usually ranges from 20 to 37 carbon atoms, with odd-numbered chain lengths predominating. The position of double bonds can be almost anywhere in the chain but is common at the 9 carbon (Blomquist and Dillwith 1985).

Hydrocarbons as Taxonomic Characters

Insects synthesize most if not all of their compliment of cuticular hydrocarbons de novo (Jackson and Blomquist 1976; Blomquist and Dillwith 1985). We can assume this synthesis is genetically controlled and affected only slightly by environmental parameters. In certain groups of insects which include termites, bees, mosquitoes, cockroaches and beetles, cuticular hydrocarbon profiles appear to have promise as taxonomic characters (Carlson and Bolten 1984; Carlson and Service 1980; Gastner and Nation 1986; Howard and Blomquist 1982; Vander Meer 1986). Howard et al. (1978) and Blomquist et al. (1979) were among the first to recognize the value of hydrocarbons as taxonomic characters. They found that the termites Reticulitermes flavipes (Kollar) (Rhinotermitidae) and Zooptermopsis angusticollis (Hagen) (Termopsidae) possess drastically different hydrocarbon profiles, and both of these differ markedly from those reported earlier for Nasuititermes exitiosus (Hill) (Nasuititermitidae) (Moore 1969). In addition, Howard and his colleagues characterized the cuticular hydrocarbons of R. virginicus (Banks) and partially characterized the hydrocarbons of five other species of Reticulitermes (Clément et al. 1985; Howard et al. 1982). In every case, hydrocarbon composition was unique.

The most thorough examination of cuticular hydrocarbons as species characters in the Coleoptera has been made by Lockey (1978, 1979a,b, 1980, 1981, 1982a,b,c). He compared the cuticular hydrocarbons of nine tenebrionid species. He found that each species has distinctive hydrocarbon compositions and congeneric species have hydrocarbon mixtures which are more similiar than those of more distantly-related species. He was able to discern a pattern in hydrocarbon mixtures of selected tenebrionid beetles which paralleled their grouping into the tribes Tenebrionini and Diaperini.

We have expanded on the early work of Blomquist et al. (1979) and characterized the cuticular hydrocarbons of the entire genus of dampwood termites, Zootermopsis (Haverty et al. 1988). We were able to correlate hydrocarbon "signatures" with a heretofore undescribed mandibular character, shape and size of the subsidiary tooth, to identify the three presently recognized species of Zootermopsis (Thorne and Haverty, In press). Furthermore, these hydrocarbon studies allowed us to recognize a new subspecies (or possibly species) of Zootermopsis. The validity of this taxon has also been implicated by studies of agonistic behavior (Haverty and Thorne, In press).

With our success in characterizing an entire genus of termites and the growing acceptance of hydrocarbons as taxonomic characters, we decided to evaluate cuticular hydrocarbons as another suite of characters in Conophthorus. In this preliminary report we examined the hydrocarbon mixtures of six species: C. ponderosae, C. radiatae Hopkins, C. cembroides Wood, C. coniperda (Schwarz), C. resinosae Hopkins, and C. banksianae. This is the beginning of an extensive investigation to determine the degree of similarity and/or diversity among species in the genus Conophthorus in North America based on cuticular hydrocarbons.

METHODS AND MATERIALS

Adult cone beetles were collected as overwintering adults from infested cones or twig terminals. Only C. ponderosae was collected from three different species of pine (Pinus ponderosa, P. lambertiana, and P. monticolae) from three different locations. Beetles were allowed to emerge from the cones or twigs. One to three days after emergence they were frozen and held at -20°C until hydrocarbons were extracted. Beetles were removed from the freezer and allowed to warm to ambient temperature. Beetles shipped from the eastern half of North America were air-dried. Cuticular lipids were extracted by immersing 15 to 50 beetles, as a group, in 10 ml of hexane for 10 min. After extraction, hydrocarbons were separated from other components by pipetting the 10-ml extract and an additional 8 ml of hexane through 3 cm of activated BioSil-A in Pastuer pipette mini-columns (Blailock et al., 1976; Haverty et al., 1988). All hydrocarbon extracts were evaporated to dryness under a stream of nitrogen and redissolved in 30 ul of hexane for GC analyses.

Gas chromatography-mass spectrometry (GC-MS) analyses were performed on a Hewlett Packard 5890 gas chromatograph equipped with a Hewlett Packard 5970B Mass Selective Detector interfaced with Hewlett Packard Chemstation computer. The GC-MS was equipped with a fused silica capillary column (30 m x 0.2 mm ID, HP-1) and operated in split mode (with a split ratio of 20:1). Each mixture was analyzed by a temperature program from 200°C to 320° at 3°C/min with a final hold of 20 minutes. Electron impact (EI) mass spectra were obtained at 70 eV. n-Alkanes were identified by comparing their retention times and mass spectra with external standards. Alkenes and methyl-branched alkanes were tentatively identified by calculating their equivalent chain lengths (Nelson and Sukkestad 1970; Jackson and Blomquist 1976). Mass spectra of methlyalkanes were interpreted as described by Nelson et al. (1972), Nelson (1978), Ponomis et al. (1978), and Blomquist et al. (1987).

RESULTS

We identified a total of 69 major individual and isomeric mixtures of hydrocarbons (mean percent $\geq$ 0.5% of the total hydrocarbon mixture) in the cuticular wax of six species of Conophthorus. The hydrocarbon components consist of n-alkanes, alkenes, alkadienes, 2- or 4-methylalkanes, 3-methylalkanes, single component and isomeric mixtures of internally-branched monomethylalkanes, dimethylalkanes and trimethylalkanes. Unique and abundant, species-specific hydrocarbon components were identified.

The normal alkane composition in all six species is a continuous series from n-heneicosane to n-tritriacontane. n-Tricosane, n-pentacosane and n-heptacosane predominate. All six species have measurable quantities of normal alkanes of even-numbered chain length from n-docosane to n-octocosane. n-Tetracosane and n-hexacosane are the most abundant even-numbered normal alkanes. With the exception of n-hentriacontane, these species contain all of the same n-alkanes components from n-heneicosane to

n-tritriacontane. C. resinosae and C. banksianae, however, contain significant amounts (≤ 1.0%) of n-hentriacontane. Usually n-alkanes have little taxonomic value because nearly all species have these components in their hydrocarbon mixtures. However, we feel n-hentriacontane could be used for species discrimination in Conophthorus.

The Conophthorus species examined in this report all have the unsaturated hydrocarbons, pentacosene and heptacosene. Other alkenes are present in very small, or trace, amounts and occur only as a shoulder of the peak of a terminally-branched monomethyl alkane. C. resinosae and C. banksianae both contain significant amounts of pentatriacontene and heptatriacontene. These hydrocarbons elute at unique times (ECL = 34.7 and 36.7, respectively) and may prove to be diagnostic for these species since they are not found in any of the other four species. C. ponderosae and C. cembroides do not contain significant quantities of alkadienes. Pentacosadiene in C. ponderosae and C. radiatae and heptacosadiene in C. coniperda coelute with a methyalkane; this makes them difficult to use for diagnostic purposes.

Terminally-branched alkanes are relatively rare in these six species of Conophthorus. Virtually none were found in C. cembroides. Significant quantities of internally-branched monomethylalkanes occur in these Conophthorus species as complex isomeric mixtures with methyl branches on odd-numbered carbons 9, 11, 13 and 15. Dimethylalkanes in insects generally have methyl branches on odd-numbered carbons separated by an odd number of carbons (Blomquist et al. 1987). All of the dimethylalkanes produced by these species of Conophthorus fit this pattern. The majority of the methyl branches are separated by three carbons and include the 3,7-dimethyalkanes (C. ponderosae from sugar pine), the 11,15- and 13,17-dimethylalkanes (C. ponderosae, C. cembroides) and 15,19-dimethypentatriacontane (C. ponderosae, C. radiatae). C. coniperda, C. resinosae and C. banksianae contain only small quantities of dimethylalkanes in their hydrocarbon mixtures, whereas C. cembroides, C. ponderosae and C. radiatae all contain significant quantities of dimethylalkanes. The hydrocarbon mixtures of C. cembroides contain significant amounts of 9,15- and 11,15-dimethylheptacosane and 11,15-; 13,17-dimethylnonacosane. These unique, species-specific dimethyalkanes with unique ECLs are not found in the other five species. We identified a homologous series of 13,17,23-trimethlyalkanes starting at the C_{36} carbon (ECL = 33.9) in C. ponderosae, C. radiatae, and possibly C. resinosae and C. banksianae. C. coniperda and C. cembroides clearly contain fewer trimethylalkanes than the other four species of Conophthorus with trimethylalkanes reported in this paper.

DISCUSSION

The cuticular hydrocarbons of the six species of Conophthorus reported in this paper, as is the case for many insect species (Blomquist et al. 1987), consist of complex mixture of straight-chained and methyl-branched, saturated components and one or more unsaturated components. The relatively large number of hydrocarbon components often found on the cuticle of insects, ease of chemical analysis and identification, and species-specific

compositions for many insects make them attractive characters for use in chemotaxonomy (Carlson and Bolten 1984; Gastner and Nation 1986; Haverty et al. 1988; Vander Meer 1986).

Cuticular hydrocarbons, particularly the unsaturated and methyl-branched components, are biosynthesized by insects (Blomquist et al. 1987). A small percentage of the n-alkanes in several species (Blomquist and Jackson 1979; Nelson et al. 1971) may arise from the diet, but unsaturated and methy-branched hydrocarbons are rare in plants. Thus, the prevalence of unsaturated and methyl-branched components in Conophthorus is fortuitous. Although it has been clearly shown that the methyl branch groups of the 3-methyl and all internally branched alkanes arise form the insertion of methylmalonyl-CoA in place of malonyl-CoA during chain elongation, it is not known how the positions and number of methyl branches are regulated to produce, what appears to be in many cases, species-specific cuticular hydrocarbon profiles. In some insects, the amino acid valine (and presumably methionine and isoluecine) serves as the precursor to the carbon skeleton of methylmalonyl-CoA (Dillwith et al. 1982; Halarnkar et al. 1985), whereas in other species succinate is converted to methymalonyl-CoA (Blomquist et al. 1980; Chu and Blomquist 1980). Regardless of the precursors and regulation, the end products appear sufficiently diverse to serve as chemotaxonomic characters in many hard-to-distinquish species.

Conophthorus is a refractory genus. Many of the species are difficult to separate on the basis of morphological characters alone. We hope to develop a new suite of characters for the entire genus, similar to our study with the dampwood termites, Zootermopsis (Haverty et al. 1988). Thus far the results are encouraging. The cuticular hydrocarbon mixtures contain diagnostic n-alkanes, alkenes, alkadienes and monomethyl-, dimethyl- and trimethylalkanes, which are useful for separation of these species.

The composition of the major cuticular wax components in three populations of Conophthorus ponderosae is complex. With one possible exception, the hydrocarbon mixtures are qualitatively the same in all three of the populations we examined: 3,7-dimethylalkanes in C. ponderosae from sugar pine. It may be possible the C. ponderosae populations we collected from ponderosa pine and western white pine produce these dimethylalkanes in insignificant quantities. Future analyses with more adults from additional populations may resolve the presence or absence of these 3,7-dimethylalkanes in C. ponderosae. If one agrees that hydrocarbon profiles are species-specific (Howard et al. 1982; Haverty et. al. 1988; Vander Meer 1986), we would infer that two populations of C. ponderosae evaluated here are the same species, or at least very closely related. C. ponderosae from these three pine species may be sibling species, subspecies or distinct populations of the same species whose cuticular hydrocarbon phenotypes have drifted apart in response to evolutionary pressures such as host, climate or geographical location.

The hydrocarbon patterns of C. resinosae and C. banksianae are qualitatively identical; no unique hydrocarbon components were found between these two species. They do possess several components which easily separate them from the other four species discussed in this paper. This evidence supports the concern that C. banksianae is not a valid species (Stephen

Wood, personal communication). Further elucidation with biological and genetic studies will be necessary to resolve this problem.

The results reported in this paper are preliminary in that we have not characterized the cuticular hydrocarbons of all of the extant species of Conophthorus nor have we examined numerous populations of each species. We could, with the data available, develop a dichotomous key to these six species. We feel it would be premature at this point in our research. We can illustrate the potential or value of cuticular hydrocarbons for developing such keys by selecting the hydrocarbons we might use (Table 1). Useful hydrocarbons should be abundant, not minor components (at least 1%, but preferably > 5% of the total hydrocarbon mixture). They should also be unique or present in only a few of the species, or conversely, they should be common in most of the species yet completely absent, rare or of insignificant quantities in one or few. Furthermore, they should have a unique elution time so that they do not coelute with another hydrocarbon in the same species nor should they elulte at a time similar to a different hydrocarbon in a different species. From a collection of these hydrocarbons, many different dichotomous keys are possible.

Future studies will involve further characterization of the cuticular hydrocarbons of additional, morphologically-distinct species of Conophthorus, and quantitative evaluation of intra- and interspecific variation. Hopefully, these studies will help clarify the taxonomy of this genus, especially the polyphagous species, C. ponderosae, and the potentially invalid species, C. banksianae and C. cembroides.

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Table 1. Diagnostic hydrocarbons identified from six species of Conophthorus.[a]

Hydrocarbon	ECL	Conophthorus species[b]					
		Cpon	Ccem	Ccon	Crad	Cres	Cban
Pentacosadiene	24.69	tr	o	o	++	++	++
Heptacosene	26.70	+	+	+++	tr	++	++
9-; 11-; 13-Methylheptacosane	27.32	+	+	+++	tr	+	+
11,15-Dimethylheptacosane + 9,15-Dimethylheptacosane	27.63	o	+++	o	o	o	o
15-Methyloctacosane	28.32	o	++	o	o	o	o
9-; 11-; 13-; 15-Methylnonacosane	29.32	o	o	++	o	o	o
11,15-; 13,17-Dimethylnonacosane	29.61	tr	o	++	o	o	o
n-Hentriacontane	31.00	o	+++	o	o	o	o
11-; 15-Methyltritriacontane	33.30	+	++	o	o	++	++
Pentatriacontene	34.70	++	++	x	tr	o	o
11-; 13-Methylpentatriacontane	35.31	tr	o	o	o	++	++
Heptatriacontene	36.70	++	++	o	++	+	+
13,17,21-Trimethylheptatriacontane	37.90	o	o	o	o	+++	+++
11-; 13-Methylnonatriacontane	39.30	++	o	x	+	++	++
13,17,23-, 13,17,25-Trimethyl nonatriacontane	39.90	++	++	o	++	+	+
		++	o	o	++	x	x

[a] A triple + indicates ≥ 5.0% , ++ from 1.0 to 5.0% and + from 0.5 to 1.0% of the total hydrocarbon component. Some trace (tr.) components appear infrequently or consistently in very small quantities (< 0.5% of the total). A zero indicates the hydrocarbon was never identified for the species. Compounds with an x were not identified for the species; mass spectra were insufficient to make a positive identification of the hydrocarbon.

[b] Cpon = Conophthorus ponderosae, Ccem = C. cembroides, Ccon = C. coniperda, Crad = C. radiatae, Cres = C. resinosae, and Cban = C. banksianae.

LITERATURE CITED

Blailock, T.T., Blomquist, G.J. and Jackson, L.L., 1976: Biosynthesis of 2-methyalkanes in the crickets Nemobius fasciatus and Gryllus pennsylvanicus. Biochem. Biophys. Res. Commun., vol 68, pp. 841-849.

Blomquist, G.J., Chu, A.J., Nelson, J.H. and Pomonis, J.G., 1980: Incorporation of [2,3-^{13}C] succinate into methyl-branched alkanes in a termite. Arch. Biochem. Biophys., vol. 204, pp. 648-650.

Blomquist, G.J. and Dillwith, J.W., 1985: Cuticular lipids. In Kerkut, G.A. and Gilbert, L.I., [eds.], Comprehensive Insect Physiology, Biochemistry and Pharmacology. Vol. 3. Integument, Respiration and Circulation, pp. 117-154.

Blomquist, G.J., Howard, R.W. and McDaniel, C.A., 1979: Structure of the cuticular hydrocarbons of the termite Zootermposis angusticollis (Hagen). Insect Biochem., vol. 9, pp. 371-374.

Blomquist, G.J. and Jackson, L.L., 1979: Chemistry and biochemistry of insect waxes. Prog. Lipid. Res., vol. 17, pp. 319-345.

Blomquist, G.J., Nelson, D.R., de Renobales, M., 1987: Chemistry, biochemistry, and physiology of insect cuticular lipids. Arch. Insect Biochem. Phys., vol. 6, pp. 227-265.

Carlson, D.A. and Bolten, A.B., 1984: Identification of africanized and european honey bees, using extracted hydrocarbons. Bull. Entomol. Soc. Amer., vol. 30, pp. 32-35.

Carlson, D.A. and Service, M.W., 1980: Identification of mosquitoes of Canopheles gambiae species complex A and B by analysis of cuticular components. Science, vol. 207, pp. 1089-1091.

Chu, A.J. and Blomquist, G.J., 1980: Biosynthesis of hydrocarbons in insects: Succinate is a precursor of the methyl-branched alkanes. Archiv. Biochem. Biophys., vol. 201, pp. 304-312.

Clément, J.L., Lange, C., Blum, M., Howard, R., and Lloyd, H., 1985: Chimosystematique du genere Reticulitermes (Isoptères) aux U.S.A. et en Europe. Actes Coll. Insectes Soc., vol. 2, pp. 123-131.

Dillwith, J.W., Nelson, J.H., Pomonis, J.G., Nelson, D.R. and Blomquist, G.J., 1982: A ^{13}C NMR study of methyl-branched hydrocarbon biosynthesis in the housefly. Jour. Biol. Chem., vol. 257, p. 11305.

Furniss, R.L. and Carolin, V.M., 1977: Western Forest Insects. U.S. Dept. Agric. Misc. Publ. No. 1339, 654 pp.

Gastner, J.L. and Nation, J.L., 1986: Cuticular lipids for species recognition of mole crickets (Orthoptera:Gryllotalpidae): II. Scapteriscus abbreviatus, S. acletus, S. vicinus, S. sp. and Neocurtilla hexadactyla. Arch. Insect Biochem. Physiol., vol. 3, p. 126-134.

Halarnkar, P.P., Nelson, J.H., Heisler, C.R. and Blomquist, G.J., 1985: Metabolism of propionate to acetate in the cockroach Periplaneta americana. Arch. Biochem. Biophys., vol. 236, pp. 526-534.

Hadley, N.F., 1982: Surface waxes and integumentary permeability. American Scientist, vol. 68, pp. 546-553.

Hadley, N.F., 1985: The adaptive role of lipids in biological systems. Wiley-Interscience Publ. New York, 319 pp.

Haverty. M.I., Page, M., Nelson, L.J. and Blomquist, G.J., 1988: Cuticular hydrocarbons of dampwood termites, Zootermopsis: intra- and intercolony variation and potential as taxonomic characters. Jour. Chem. Ecol., vol. 14, pp. 1035-1058.

Haverty, M.I. and Thorne, B.L., 1989: Agonistic behavior correlated with hydrocarbon phenotypes in dampwood termites, Zootermopsis (Isoptera: Termopsidae). Jour. Insect Behavior (In press).

Hedlin, A.F., Yates III, H.O., Tovar, D.C., Ebel, B.H., Koerber, T.W. and Merkel, E.P., 1980: Cone and seed insects of North American conifers. Canadian Forestry Service, 122 pp.

Howard, R.W. and Blomquist, G.J., 1982: Chemical ecology and biochemistry of insect hydrocarbons. Ann. Rev. Entomol., vol. 27, pp. 149-172.

Howard. R.W., McDaniel, C.A. and Blomquist, G.J., 1978: Cuticular hydrocarbons of the eastern subterranean termite, Reticulitermes flavipes (Kollar) (Isoptera:Rhinotermitidae). Jour. Chem. Ecol., vol. 4, pp. 233-245.

Howard, R.W., McDaniel, C.A., Nelson, D.R. Blomquist, G.J., Gelbaum, L.T. and Salkow, L.H., 1982: Cuticular hydrocarbons as possible species and caste-recognition cues in Reticulitermes sp. Jour. Chem. Ecol., vol. 8, pp. 1227-1239.

Jackson, L.L. and Blomquist, G.J., 1976: Insect waxes, In Kolattududy, P.E., (ed.), Chemistry and Biochemistry of Natural Waxes. Elservier, Amersterdam, pp. 201-233.

Jenkins, M.J., 1982: Western white pine: the effect of clone and cone color on attacks by the mountain pine cone beetle. Ph.D. Thesis, Utah State Univ., Logan, Utah, 91 pp.

Lockey, K.H., 1978: Hydrocarbons of adult Tribolium castaneum Hbst. and Tribolium confusum Duv. (Coleoptera:Tenebrionidae). Comp. Biochem. Physiol., vol. 61B, pp. 401-407.

Lockey, K.H., 1979a: Cuticular hydrocarbons of adult Aliphitophagus bifasciatus (Say) and Aliphitobius diaperinus. (Parz.) (Coleoptera: Tenebrionidae). Comp. Biochem. Physiol., vol. 64B, pp. 47-56.

Lockey, K.H., 1979b: The adult cuticular hydrocarbons of Tenebrio molitor L. and Tenebrio obscurus F. (Coleoptera:Tenebrionidae). Insect Biochem., vol. 8, pp. 237-250.

Lockey, K.H., 1980: Cuticular hydrocarbons of adult Blaps mucronata Latreille (Coleoptera:Tenebrionidae). Comp. Biochem. Physiol., vol. 67B, pp. 33-40.

Lockey, K.H., 1981: Cuticular hydrocarbons of adult Cylindrinotus laevioctostriatus (Goeze) and Phylan gibbus (Fabricius) (Coleoptera: Tenebrionidae). Insect. Biochem., vol. 11, pp. 549-561.

Lockey, K.H., 1982a: Cuticular hydrocarbons of adult Onymacris marginipennis (Breme) (Coleoptera:Tenebrionidae). Comp. Biochem. Physiol., vol. 73B, pp. 275-282.

Lockey, K.H., 1982b: Hydrocarbons of adult Onymacris plana (Peringuey) and Onymacris rugatipennis (Haag) (Coleoptera:Tenebrionidae). Insect Biochem., vol. 12, pp. 69-81.

Lockey, K.H., 1982c: Hydrocarbons of adult Physadesmia globosa (Haag) and Stenocara gracilipes (Haag) (Coleoptera:Tenebrionidae). Insect Biochem., vol. 12, pp. 331-342.

Mayr, E., 1969: Principles of Systematic Zoology. McGraw-Hill Book Co., New York, 428 pp.

Moore, B., 1969: Biochemical studies in termites, In Krisnna, K. and Weesner, F.M., [eds.], Biology of Termites. Vol 1, Academic Press. New York, pp. 407-432.

Nelson, D.R., 1978: Long-chained methyl-branched hydrocarbons: occurance biosynthesis and function. Adv. Insect Physiol., vol. 13, pp. 1-33.

Nelson, D.R. and Sukkestad, D.R., 1970: Normal and branched aliphatic hydrocarbons from the eggs of the tobacco hornworm. Biochemistry, vol. 9, pp. 4601-4611.

Nelson, D.R., Sukkested, D.R. and Terranova, A.C., 1971: Hydrocarbon composition of the integument, fat body, hemolymph and diet of the tobacco hornworm. Life Science, vol. 10, pp. 411-419.

Nelson, D.R., Sukkestad, D.R. and Zaylskie, R.G., 1972: Mass spectra of methyl-branched hydrocarbons from eggs of the tobacco hornworm. Jour. Lipid Res., vol. 13, pp. 413-421.

Pomonis, J.G., Fatland, C.F., Nelson, D.R. and Zaylskie, R.G., 1978: Insect hydrocarbons. Corroboration of structure by synthesis and mass spectrometry
of mono- and dimethylalkanes. Jour. Chem. Ecol., vol. 4, pp. 27-39.

Thorne, B.L. and Haverty, M.I., 1988: Accurate identification of Zootermopsis species (Isoptera:Termopsidae) based on a mandibular character of non-soldier castes. Ann. Entomol. Soc. Amer., (In press).

Vander Meer, R.K., 1986: Chemical taxonomy as a tool for separating Solenopsis sp. In: Fire Ants and Leaf Cutting Ants: Biology and Management. Lofgren, C.S., Vander Meer, R.K., [eds.], Westview Press, Boulder, pp. 316-326.

Williamson, D.L., Schenk, J.A. and Bun, W.F., 1966: The biology of Conophthorus monticolae in northern Idaho. Forest Science, vol. 12, pp. 234-240.

Wood, S.L., 1982: The bark and ambrosia beetles of North and Central America (Coleoptera:Scolytidae), a taxonomic monograph. Great Basin Naturalist Memoirs, No. 6, 1359 pp.

TECHNICAL SESSION II:

Insect Biology

Moderator: Dr. Jean Turgeon, Sault Ste. Marie, Ontario, CANADA

NEW RESULTS AND SOME THINKINGS ABOUT SIGNIFICANCE AND INDUCTION OF PROLONGED DIAPAUSE IN CONE INSECTS WITH PARTICULAR REFERENCES TO THE LARCH CONE FLY (*Lasiomma melania*) AND TO THE DOUGLAS-FIR SEED CHALCID (*Megastigmus spermotrophus*)

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Summary

Occurence of prolonged diapause in european Cone and Seed Insects is restricted to the single Stenoconobiont species, that cannot develop in an alternative substrate 55 % of these insects, at least, present the capability to stay in larval or pupal diapause over more than one year. In the larch cone fly and in the Douglas-fir seed chalcid, the percentage of larvae entering prolonged diapause is inversely related to the rate of change in cone (seed for the 2nd species) yield from one year to the next. Prolonged diapause appears as an adaptative mechanism allowing a short-term adjustment of insect population to host abundance. Diapause induction does not seem to consist of a single model, but likely proceeds from a combination of various factors, as well endogenous as exogenous. Various hypotheses are suggested: chemical signals provided by the tree, joint effect of climatic factors on larval development and initiation of the future crop, influence of previous prolonged diapause in the mother generation. However, the long-term efficiency of this mechanism seems limited in regard to both the mortality of diapausing insects and the rougher synchronization of diapause termination with host abundance. It tends to guarantee the species perenniality, through a minimal population, rather than to maintain the original population.

Introduction

Phytophagous insects developing in cones and seeds of Conifers generally encounter very irregular fluctuations in host abundance from year to year, including total crop failures (Fenner, 1985) . Janzen (1971) assumed this acyclism in cone occurence, defined as "masting" by Fenner, to correspond to an evolutionnary response of trees to predation on their reproductive structures. However, some insect species have also been known for a long time for having evolved adaptative strategies to compensate for these cone crop variations. The main strategy appears to be prolonged diapause. The corresponding insects are capable to extend their winter rest, that generally corresponds to an obligatory diapause broken by low temperatures (Nesin, 1984) , over several more years (up to 7 years in *Plemeliella abietina* Seitner, Annila, 1981, 1982) .

Various observations clearly revealed the adaptative nature of this mechanism, that theoretically permits survival of insect populations during periods of low food supply. Thus, inverse correlations between the induction of prolonged diapause and cone crop (or seed crop) size the year following larval feeding have been noticed, for instance, in Cydia strobilella L. and Kaltenbachiola strobi Winn. in Norway (Bakke, 1963) , Megastigmus spermotrophus Wachtl. and M. specularis Walley in Finland (Annila, 1982) , Barbara colfaxiana Kearfoot in Canada (Miller and Hedlin, 1984) , Megastigmus suspectus Borries var. pinsapinis Hoffm. in France (Fabre, 1986) . However, such precise connections have not been observed in a few cases, especially in some insects strictly related to seeds (Plemeliella abietina Seitn. in Finland, Annila, 1984; Kaltenbachiola strobi Winn. in the Soviet Union, Stadnitskii, 1986; Contarinia oregonensis Foote, Miller and Hedlin, 1984).

Nevertheless, most studies only deal with the place of prolonged diapause within punctual relationships established between one or more insect species and a coniferous tree. In view of understanding general cone-insect coevolution processes, it appears therefore interesting to consider how the prolonged diapause phenomenon is distributed among all the insect species constituting the phytophagous fauna colonizing cones in a same biogeographic area, especially in regard to both insect dependance on cones and Conifer Evolution. Data previously collected upon cone insect fauna of Conifers growing in Western Europe (Roques, 1983) will be here treated in this way.

On the other hand, factors really inducing prolonged diapause as factors acting on its termination are still poorly unde stood in most species. We shall present some recent results obtained upon two cone insect species, i) the larch cone fly, Lasiomma melania Ackl. (Diptera, Anthomyiidae) specific to cones of Larix species (Roques, 1983) , ii) the Douglas-fir seed chalcid, Megastigmus spermotrophus Wachtl. (Hymenoptera, Torymidae) , specific to seeds of Pseudotsuga species but introduced from North America to Europe with its main host (P.menziesii) (Roques, 1981) . These results will conduct us to deliver more general thinkings on the real part played by prolonged diapause in cone insect populations dynamics.

A dominant and exclusive feature of insects strictly related to cones

59 phytophagous species have been presently identified as cone-eaters in Western Europe (Roques, 1983) . Among them, insects presenting the capability of prolonged diapause belong to the single Stenoconobiont group, i. e. species that can develop only in the cones. None of the 17 Heteroconobiont species, that are alternatively able to attack other tree structures, shows prolonged diapause habits. Among the 42 Stenoconobiont species, more than a half at least (23, i. e. 55% to our present knowledge) may conversely enter diapause for more than one winter (Table 1).

Occurence of prolonged diapause in Conobionts therefore appears all the more as effective as adaptation to host is close. It is not surprising that it corresponds to a general feature in all species whose larval development completely takes place within seeds (some Cecidomyiids, seed chalcids) , and thus fully undergo the selection pressure from the host without possibilities of escaping.

It must also be noticed that most Stenoconobionts (18/23, i. e. 78%) colonizing Conifer species with an annual development cycle for Seed-Cone, like Abietaceae of genus Picea, Larix, Abies, possess this capability. By contrast, prolonged diapause habits are shown by a minority (5/19, i. e. 26%) of the insects damaging cones of Conifer species with a pluriannual development cycle for Seed-Cone (Pinus, Juniperus) . Many of these last insects exhibit other adaptative features, that seem more archaic

(extended life-span, polyvoltinism) . Therefore, the set-up of prolonged diapause mechanism could have been related to the appearance of advanced forms of Conifers presenting annual development cycle for Seed-Cone.

Table 1 : Occurence of prolonged Diapause in west european Conobionts in regard to cone-insect relationship, insect feeding pattern and coniferous host species.

Nature of Cone-Insect Relationships	Prolonged diapause	No Prolonged diapause	Total
Stenoconobionts	23	19	42
Heteroconobionts	0	17	17
Seminiphagous species	13	2	15
Conophagous species	0	17	17
Conoseminiphagous species	14	13	27
Stenoconobionts developing in Picea, Abies, Larix	18	5	23
Stenoconobionts developing in Pinus, Juniperus	5	14	19

Prolonged diapause - cone crop variations, some supplementary evidences for their adaptative relationships

Table 2 presents the diapausing habits of the european Megastigmus species. The single species damaging Conifers whose seed crop varies dramatically from year to year show a tendency to prolonged diapause. Insects infesting tree species that nearly always bear a minimal annual cone crop in natural stands (Cypress, Junipers) do not generally present diapausing individuels. However, potentialities for prolonged diapause are more important than the ones naturally expressed in these last species. For instance, the mediterranean Cypress seed-chalcid, M.wachtli, may show a large diapause rate when developing in artificial cypress stands growing in climatic conditions unfavourable for annual fructification (Roques and Raimbault, 1986) .

Table 2 : Occurence and usual Duration of prolonged Diapause in european species of Megastigmus (Hymenoptera, Torymidae) related to Conifer seeds, in regard to cone crop fluctuation pattern of their respective host.

SPECIES	HOST	MEAN TIME BETWEEN TWO ABUNDANT CROPS	OCCURENCE AND POSSIBLE DURATION OF PROLONGED DIAPAUSE
M. amicorum	Juniperus oxycedrus	annual *	very scarce, 1 year
M. bipunctatus	Juniperus communis	1-2 years *	very scarce, 1 year
M. pictus	Larix decidua	3-10 years *	very frequent, 1-3 years
M. spermotrophus	Pseudotsuga menziesii	3-11 years *	very frequent, 1-5 years
M. strobilobius	Picea abies	3-5 years *	very frequent, 1-5 years
M. suspectus	Abies alba	2-3 years *	very frequent, 1-5 years
M. suspectus var. pinsapinis	Cedrus atlantica	3 years * *	very frequent, 1-3 years
M. wachtli	Cupressus sempervirens	annual *	very scarce, 1 year
M. aculeatus	Rosa spp.	1 to 2 years *	null
M. brevicaudis	Sorbus spp.	annual *	null

* after USDA, 1974
* * after Toth, 1984

Results from a 12-year survey of L.melania populations in the French Alps confirms this adaptative nature (Roques, 1986a). The mean percentage of larvae entering prolonged diapause in a given year varies from 5 to about 50%. No significant relationship can be established between prolonged diapause and the size of the current cone crop. However, the incidence of prolonged diapause is inversely correlated with the rate of change in cone yield from one year to the next and, less significantly, with the size of the cone crop the following year (Figure 1).

Similar results have been previously detailed for M.spermotrophus in Douglas-fir stands located in Southwestern France (Roques, 1986b).

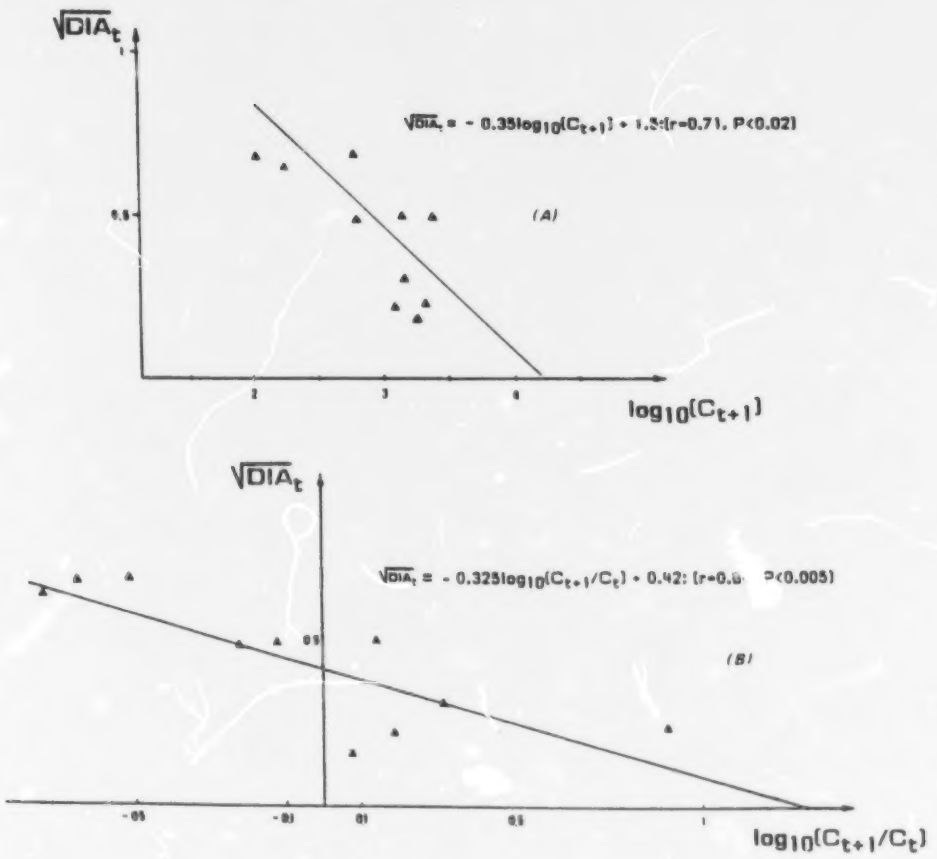

Figure 1 : Relationships between the annual percentage of larvae entering prolonged diapause in L. melania (DIA_t) and some variables related to cone crop evolution.
-a) Size of the cone crop the following year: -b) Rate of change in cone yield from one year to the next. Values measured during ten consecutive years (1975-1985) in a same larch stand located in the Southern French Alps (Briançon), at 1200m altitude.
DIA_t is estimated from a total of 500 individuals per year: Cone crop by the mean number of cones per tree, counted of the 50 same trees. Square root and logarithmic transformation are used to stabilize variance.

Consequently, the percentage of larvae entering prolonged diapause in these two last species within a given stand is essentially related to the relative importance and to the direction of the future cone crop fluctuation.

Theoretically, this mechanism enables the main part of a generation to survive during extended periods of crop failures, but it must be noticed that 10% of the populations emerge, at least, in L.melania as in M.spermotrophus the year following larval development, even in case of null crop (Roques, 1986a, 1986b).

How to explain these correlations? two kinds of hypotheses have been generally assumed: 1) A coinciding action of same weather factors, but inducing adverse effects, on the two phenomena; 2) A direct effect from the tree, that would provide insect larvae with chemical information on the relative importance of the future crop comparatively to the current crop.

Is coinciding effect of climatic factors on both diapause induction and future cone crop initiation fully explaining, and also realistic, in L. melania and M. spermotrophus?

In L. melania, the annual percentage entering diapause in the surveyed larch stands is effectively correlated with the values measured for certain weather factors during larval feeding (June-July) . A positive relationship is noticed with solar insolation and a negative one with total rainfall (Figure 2) . Temperature seems to have marginal effect, that confirms previous findings from Nesin (1984) . On the other hand, the period corresponding to initiation and differentiation of seed-cone buds, subsequently developing in cones the following year, in larch (according to Barner and Christiansen, 1960) coincids quite perfectly with larval development in larch cone fly (Roques, 1986).

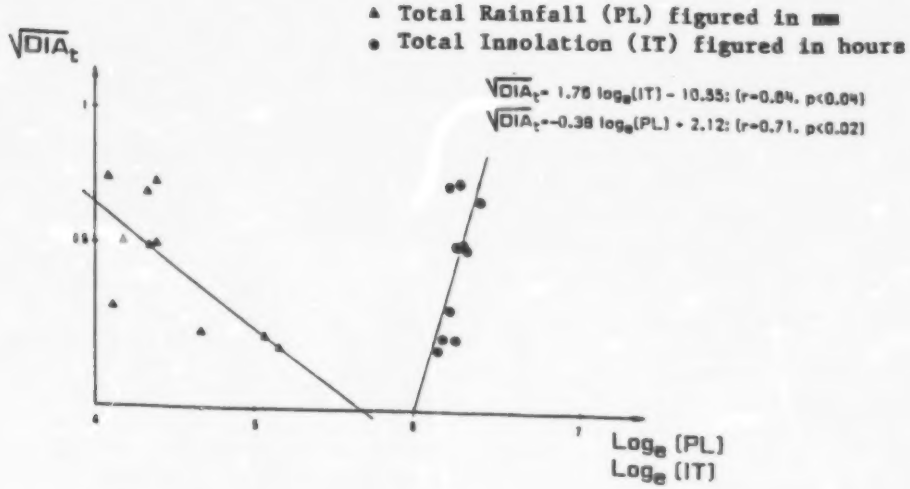

Figure 2 : Relationships between the annual percentage of larvae entering prolonged diapause in L. melania (DIA_t) and some weather variables, -a) total insolation (TI) measured during larval feeding period; -b) total rainfall (TR) during the same period; Experimental conditions and Statistical analysis similar to those detailed in Figure 1.

In M. spermotrophus, the percentage of prolonged diapause is linked to the temperature values observed during larval feeding, according to Hussey (1955) . Temperature also seems to influence, at least partially, initiation of female primordia in Douglas-fir (Lowry, 1966; Allen and Owens, 1972; Eis, 1973) . Not enough data were collected in Douglas-fir to confirm these latter observations but they obviously tend to comfort the assumption of a coincident and adverse effect of weather factors on insects and cone crop.

However, this is a reasonable but limited explanation. Various patterns of Seed-Cone bud development exist in Conifers. Time of primordia initiation and female bud differentiation especially vary among tree species, though normally occuring in the season preceding pollination (Allen and Owens). Conversely to the process observed in larch, this differentiation, and thus the potential importance of the next crop, appears to be achieved in some tree species previously to the arrival and larval development of cone insects. This is especially observed in the Pseudotsuga-M. spermotrophus system, where larval development and undifferenciated buds are synchronous only a few time, generally less than 10 days (Figure 3) . It seems unlikely that the adverse relationship previously observed is the result of coinciding effect of temperature variations occuring during these few days. However, an effect of subsequent climatic accidents (summer drought for instance, Ebell, 1971) on both larval development and maintenance of the pre-determined quantity of female buds cannot be excluded.

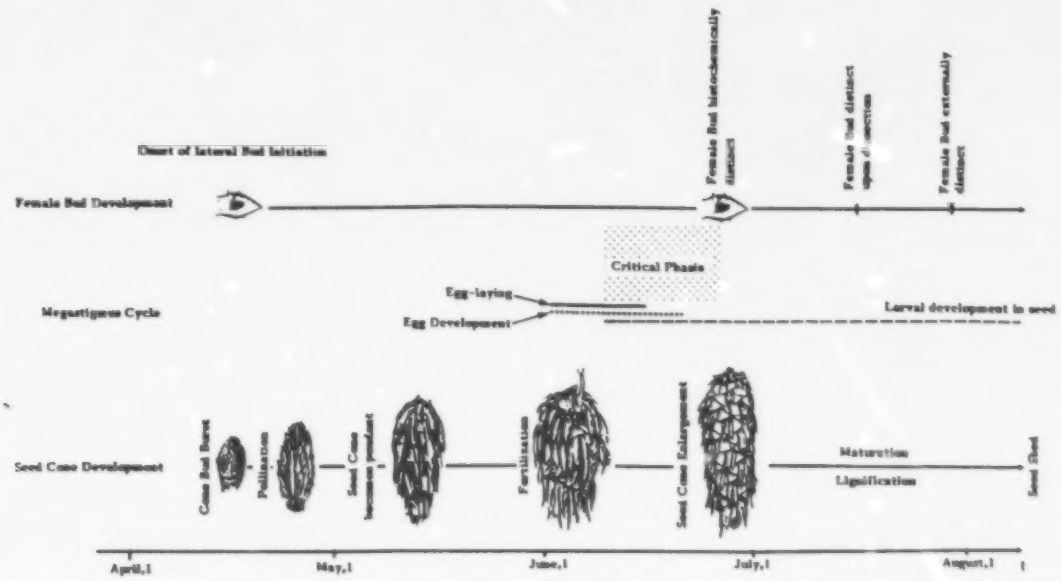

Figure 3 : Life history of female reproductive structures in Douglas-fir compared to the life cycle of the Douglas-fir seed chalcid, M. spermotrophus, within Douglas-fir stands located in Central France (Orléans).

Therefore, could the tree induce prolonged diapause through chemicals offered to insects during larval feeding in cones?

According to Allen and Owens (1972), cone crop fluctuations in Douglas-fir could result from a more or less important differentiation of axillary bud primordia in female bud rather from the variations in the number of initiated primordia, that appears annually stable. Hormones and Nutrients acting during the differentiation phasis appear therefore essential. This period largely coincids with the growth phasis of current year cones. Cone growth and Cone maturation have been shown to occur in competition with the other vegetal processes, all the tree structures using the same photosynthetates (Dickman and Kozlowski, 1968). The more rapid period of growth of subtending cones would especially serve as a "sink" for nutrients, minerals and hormones, diverting these chemicals from bud initiation pathway. Thus, a heavy current crop tends to develop contradictorily to an important female bud initiation (Allen and Owens, 1972; "negative feed-back" in Mattson, 1972) . This could explain, in part, why abundant cone crop do not occur in successive years.

Is it unrealistic to consider that, following an evolutionary process, this rule of negative feed-back could be perceptible to larvae through peculiar nutritional conditions occuring when cone crop is heavy?

What would be the possible cues ? A higher rate in some nutrients or a different ratio between some of them, when the crop is heavy? Presence or, conversely, absence of some chemicals, especially hormones, in the same situation ?

Miller and Hedlin (1984) listed some compounds known to be associated with reproductive bud initiation (elevated nitrogen, especially arginine, and carbohydrates levels: gibberellic acids) but the critical lack in tree physiology studies dealing with pathways of chemicals utilization during cone development today prevents a further formulation of possible assumptions.

Some limited experimental studies have been performed in order to detect possible tree influence on prolonged diapause initiation in M. spermotrophus. Repeated observations of large differences in larval dimensions, when examining X-ray photographs of mature larvae collected in the same orchard, suggested possible relation with diapausing behaviour, that would have been based upon divergent nutritionnal qualities of the food (seed). Individual rearings of corresponding larvae have not revealed any difference between diapausing and non-diapausing insects but, conversely, differences related to the sex of future imagos (Table 3).

Table 3 : Comparison of dimensions in mature M. spermotrophus larvae in regard to the sex of future corresponding imagos and to their diapausing habits. Measurements were realized using X-ray photographs of 200 larvae collected in the same stand (Lavercantière 1986).

	Diapausing larvae		Non-diapausing larvae		Larvae developing into males		Larvae developing into females	
	Mean	sd	Mean	sd	Mean	sd	Mean	sd
Length	0.270	0.084	0.288	0.053	0.230	0.030	0.312	0.038
Width	0.121	0.030	0.119	0.028	0.099	0.012	0.143	0.023

Other experiments were carried out in 1987 in order to artificially modify the importance of the future crop in some trees, thus allowing to look at possible modification in diapause induction. Ten ramets presenting heavy cone crops and located within the same clonal seed-orchard (Ingrannes_Central France), have been treated before Megastigmus egg-laying in various ways known to stimulate female bud initiation (Allen and Owens, 1972) : girdling: fertilization using Nitrate-nitrogen: removal of all the developing cones, excepted one, from each branch. Objectives were to maintain the importance of cone crop, at least, in these trees the following year. Therefore, the percentage of prolonged diapause in their colonizing larvae could have been compared with the one observed in control ramets of the same clones and showing a current crop of equal importance, consequently tending to drop the following year. Unfortunately, treatment methods did not succeed in maintaining the crop, 1988 crop appearing as a total failure in all trees. This experimentation is nevertheless interesting to be repeated.

Anyhow, this presumed tree effect is unlikely to explain the whole complexity of diapause process. As a matter of fact, the observed relationship between production and diapause at stand level recovers a large diversity in diapausing habits at inferior levels.

Some observations about heterogeneity of diapausing habits in M. spermotrophus within a same stand populations

Lavercantière Douglas-fir seed orchard (Southwestern France) provides a demonstrative example. Since its first flowering, each cone-bearing ramet has been annually sampled and its corresponding Megastigmus population individually followed in all its biological characteristics (Percentage of damaged seeds, percentage of prolonged diapause, date of emergence and sex of diapausing individuals). At the same time, the whole crop has been annually removed from the orchard, so that successive damage resulted form re-colonization realized by populations from surrounding stands (Roques and Raimbault, 1986). A relative homogeneity in microclimatic conditions has been also ensured by mechanical treatments (Tree pruning resulting in small trees, spacing....). Therefore, the single tree-insect interactions would theoretically remain and possible differences differences would proceed from divergent evolution in their seed crop. Other results have been obtained.

The mean diapause rate annually observed at stand level effectively tends to be adversely related to the importance of the future seed crop expected at the same level (Table 4).

Table 4 : Comparison of the average percentage of prolonged diapause observed at stand level with the change in seed yield from one year to the next in 1984,1985,1986 at Lavercantière Douglas-fir seed orchard.

	Average Percentage of prolonged diapause	Seed Production Ratio Year n / Year n+1
1984	0.365	0.74
1985	0.110	2.42
1986	0.131	2.35

However, regression analysis of the mean percentage of prolonged diapause observed within each ramet against the rate of change in cone yield from one year to the next in the same ramet does not provide any significant result in the 3 analyzed years. Large differences between ramets explain this result. In some of them, chalcids appear to behave contradictorily to the general trend showed by the most part of the orchard population, as well when crop decreases as when it increases (Figure 4).

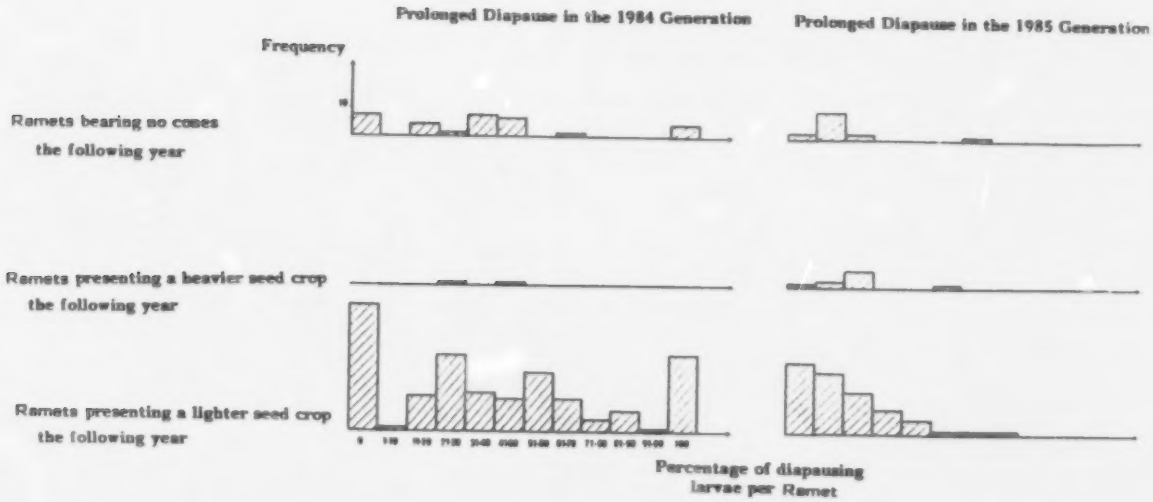
Prolonged Diapause in the 1984 Generation
Prolonged Diapause in the 1985 Generation
Frequency
Ramets bearing no cones the following year
Ramets presenting a heavier seed crop the following year
Ramets presenting a lighter seed crop the following year
Percentage of diapausing larvae per Ramet

Figure 4 : Between-ramets Variation of the average percentage of Douglas-fir seed chalcid larvae entering prolonged diapause in 1984 and 1985 in regard to the direction of the future fluctuation in seed crop of the subtending ramet within Lavercantiére Douglas-fir seed orchard (Southwestern France).

Mapping of geographical distribution of mean percentage of diapause per ramet within the orchard provides suppementary information. The heterogeneity seems to be linked to the presence of a limited number of ramets, that are geographically aggregated (Figure 5). In these ramets, most insects present "abberant" diapausing habits in regard to the future seed crop expected as well as orchard level as at tree level.

Thus, most larvae developing in 1984 within seeds beared by ramets arranged in areas 1,2,3,4 turned to adults in 1985 conversely to the pattern showed by the majority of the other larvae, whereas orchard seed crop showed a 26 % decrease and the seed crop in their own ramet generally became null. Conversely, numerous larvae of 1985 generation present in areas 5,6,7,8 entered diapause while most of the remaining others emerged in 1986 in coincidence to a notable increase in seed crop at orchard level and to a stabilization in seed crop in their own ramet. A similar process occured in 1986. These differences appear independant from clonal composition.

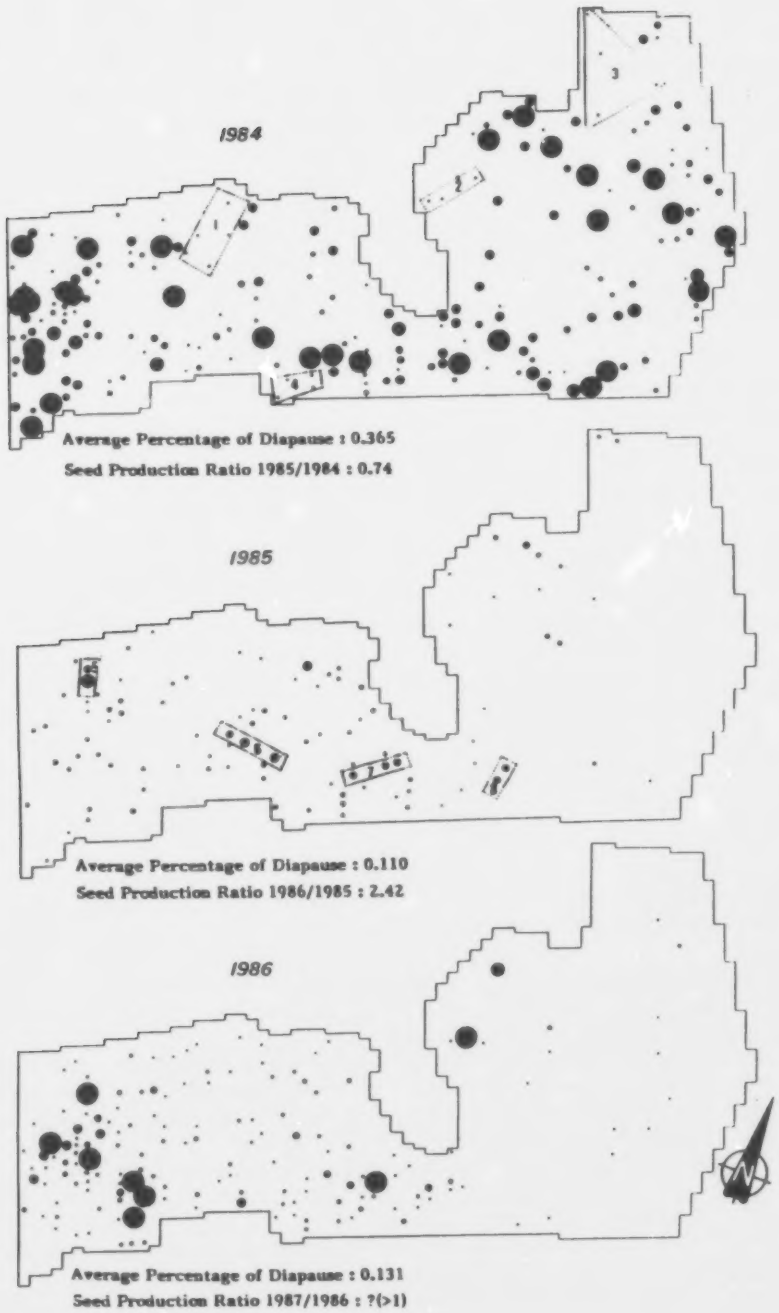
1984
Average Percentage of Diapause : 0.365
Seed Production Ratio 1985/1984 : 0.74
1985
Average Percentage of Diapause : 0.110
Seed Production Ratio 1986/1985 : 2.42
1986
Average Percentage of Diapause : 0.131
Seed Production Ratio 1987/1986 : ?(>1)

Figure 5 : Distribution maps of the average percentage of Douglas-fir seed chalcid larvae entering prolonged diapause per ramet within Lavercantière Douglas-fir seed orchard, from 1984 to 1986. Each cone-bearing ramet is represented by a circle, whose diameter is proportionnal to the importance of prolonged diapause in corresponding insects.

Diversity in larval behaviour regarding prolonged diapause is also noticeable within cones in some peculiar ramets, without apparent relationship with seed crop evolution of the tree (Figure 6). Bakke (1963) and Miller and Hedlin (1984) recorded similar facts in Cydia strobilella within spruce cones in Finland and Barbara colfaxiana within Douglas-fir cone in Canada, respectively. These authors concluded that tree do not cue larvae on its future crop.

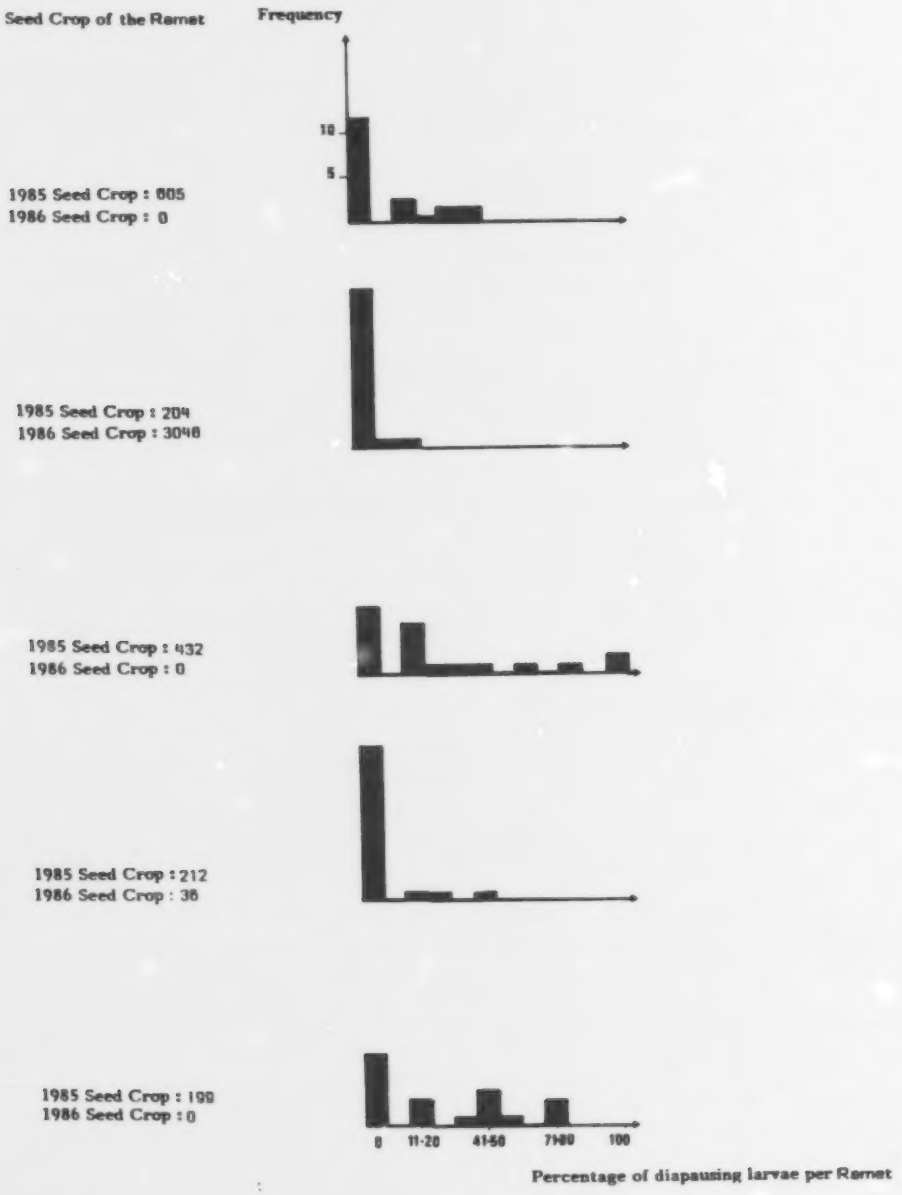

Figure 6 : Between-cones Variation of the average percentage of M. spermotrophus larvae entering prolonged diapause in 1985 within five ramets characterized by their divergent cone crop fluctuation from 1985 to 1986 in Lavercantière Douglas-fir seed orchard.

An other hypothesis : Parental effect

Aggregative distribution of trees, cones and seeds where a minority of insects behave differently in regard to diapause, and this independently from cone crop variations suggest this diversity to be related to females origin. Egg-laying are effectively aggregated most times (Hussey, 1955). Lessmen already noticed similar variations in larval diapause in experiments using females from different geographical origins. He only attributed these differences to possible genetical polymorphism in Megastigmus populations. Here, mother populations may also correspond to a combination of diapausing and non-diapausing genetical strains. However, The very limited distribution of Douglas-fir trees round the orchard (less than 500 cone mature trees within a radius of 50 kilometers) is susceptible to limit genetical diversity, by reason of limited mixing. A complementary explanation must be looked for.

Some other forest insects exhibiting prolonged diapause have been suggested to relate this capability to previous parental experience regarding diapause (Diprion pini, Geri and Goussard, 1988). Females terminating diapause would tend to generate non-diapausing larvae whereas insects ineluctably seem to enter prolonged diapause when they pass through several successive generations without diapausing. A similar phenomenon could mainly explain the diversity in diapausing habits observed within the orchard. Thus, a part of larval population, issued from non-diapausing females, could be more sensitive to the effect of factors tending to synchronization between diapause and seed crop. The other part, issued from females terminating diapause, would emerge the following year irrespective of crop fluctuations. This could explain the regular annual exit of 10 % of the individuals, at least, that has been previoulsy noticed. Diversity observed among cones of a same tree could also be refered to egg-laying by several females with different previous experiences.

These assumptions still remain formal ones, no experimental study having been conducted. Following of individual females and their subsequent breed when reared in controlled cone crop fluctuations is urgently needed.

Prolonged diapause termination

Synchronization between the importance of the current crop and diapause termination seems less adjusted in the two species (Roques, 1986a, 1986b, 1988). However, such relations have been measured under artificial rearing conditions, that largely differ from natural ones. Therefore, these results likely distort the reality. Under these breeding conditions, most imagos emerge during the 2 years following egg-laying, although some individuals emerged 3 or 4 years later. Conversely, Annila (1982) noticed the emergence of diapausing insects to be related to current crop size in M. spermotrophus in Finland, when cone and seeds are replaced in forest litter each winter.

Therefore, it is not surprising that factors involved in terminating diapause are still poorly understood. It seems, nevertheless, difficult to imagine other factors than climatic ones. Diapausing insects stay either in pupae hidden in the litter (Lasiomma) or within seeds generally fallen on the ground (Megastigmus), but out of tree action range and, consequently, out of the initiation process of the future crop. Miller and Ruth (1986) considered the temperature occuring during female bud differentiation to be involved in terminating diapause in Barbara colfaxiana. We just started similar experiments in M. spermotrophus. Lots of 50 seeds containing one-year diapausing larvae have been continuously exposed to various temperatures (15°,20°,25 respectively) during a period coinciding with female bud initiation in Douglas-fir. Results are not yet known.

What is the real incidence of prolonged diapause in population dynamics ?

Fast recovering observed in populations of L. melania and M. spermotrophus when cone crop increases again following a shortage is obviously caused by the emergence of insects diapausing since 1 year, at least (Roques, 1986a, 1988). This emergence is reduced in regard to the importance of populations that entered diapause the previous years (Roques, 1988). The duration of our study in L. melania allows to say that a part of this diapausing population never emerges.

In order to assess the importance of mortality during the first overwintering in the two considered species, pupae or damaged seeds have been laid in forest conditions. Apart from many non-recovered individuals, that have been likely destroyed by micromammals, the joint action of rodents, birds and entomopathogenous fungi is directly estimable to reduce the populations of both species in a drastical way (Figure 7).

This fact has already been noticed by Hussey (1956) in M. spermotrophus. It is likely that this mortality effect is multiplied by the duration of diapause, the more as this stay thus recovers the maximal activity period of predators (spring, summer), that is avoided during a single overwintering. Though we did not extend the studies over several years, it seems possible to conclude that the number of surviving individuals is drastically reduced after two years and the correlative further emergence very limited.

An important desynchronizing factor : late frosts

Late frosts may play an important part in desynchronizing fluctuations of cone crops and larch cone fly populations. Massive destruction of cones is often induced by these frosts, while insect emergence does not seem to be affected. When the initial cone production is high, most diapausing insects emerge normally and cannot compensate for cone reduction caused by late frosts. These climatic accidents, which are particularly prevalent at high altitude, could be one cause for the lower populations observed in this zone in L. melania (Roques, 1988).

Conclusion

These results lead to undervalue the significance of prolonged diapause in population dynamics of Conobionts. It appears as an adaptative mechanism that allow a short-term adjustment of Stenoconobionts populations to host abundance. Ensuring a part of insect population to reserve in response to the perception of a future decrease in cone crop, it limits the inter- and intraspecific competition, that becomes the more important as resources drop. However, its long-term efficiency seems limited, in regard to both the mortality of diapausing insects and the rough synchronization of diapause termination with cone abundance. It tends to guarantee the species perenniality, through a minimal population, rather than to maintain the original population.

Diapause induction does not seem to consist of a single model, generalizable to all insect species but likely proceeds from a combination of various factors, as well endogenous as exogenous.The various hypotheses suggested from our observations and limited experimentations have to be verified.

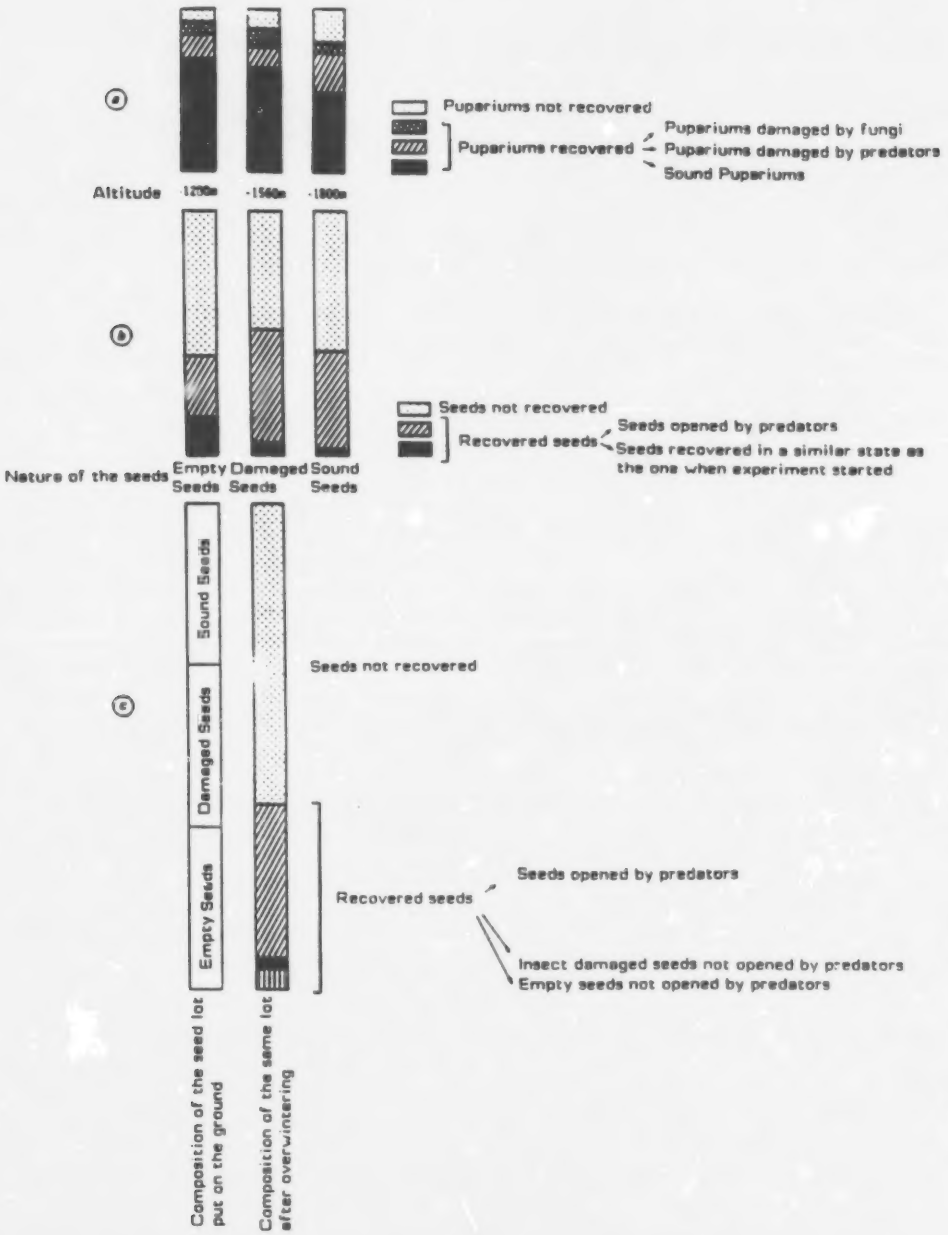

Figure 7 : Mortality observed during overwintering experiments in L. melania and M. spermotrophus.

-a) Overwintering Mortality and its pres ned reasons observed in lots of 25 puparia hidden in the forest litter in 3 stands located at various altitudes in the Southern French Alps. Puparia hidden on October, 21 1986 and recovered on May, 5 1987:

-b) Respective Importance of Predation in 3 lots of 75 overwintering Douglas-fir seeds presenting different status (empty, sound and with a Megastigmus larva inside) ,that have been separately laid on the ground on November, 7 1986 in Ingrannes seed-orchard (Central France) and recovered on April, 21 1987:

-c) Importance of Predation on a lot of 150 overwintering Douglas-fir seeds, consisting of a mixture of empty, sound and Megastigmus-damaged seeds in equal number, that has been laid on the ground in Ingrannes seed-orchard on November,7 1986 and recovered in the same conditions as in b).

A strong relationship exists between compensative capacities of insects and their presence in the tree. Precise when insect and tree are directly connected through the cone (diapause induction), the relationship becomes rougher when this connection is broken by reason of either the insect (pupation within the litter) or the vegetal (cone or seed fall). Is it possible to assume, following Janzen (1971), that this latter process corresponds to an overevoluted mechanism, allowing the protection of tree reproductive structures when insects partially compensate for crop fluctuations? If this hypothesis is the right one, it cannot be excluded that the subsequent selection pressure tends to favour genotypes more adapted in crop fluctuation compensation, especially in diapause termination synchronization. However, a second protective barrier today exists paradoxically constituted of climatic accidents, by reason of their desynchronizative effect. Individual variability in diapausing habits may, nevertheless, counterbalance this effect and permit a minimal population survival in all cases.

References

Allen G.S. and J.N. Owens, 1972. The life history of Douglas-Fir. Environnement Canada. Forestry Service. Ottawa., 139 pp.

Annila E., 1981. Fluctuations in cone and seed insect populations in Norway spruce. Comm. Inst. For. fenn., 101 : 1-32 (In Norwegian).

Annila E., 1982. Diapause and population fluctuations in Megastigmus specularis Walley and Megastigmus spermotrophus Wachtl. (Hymenoptera, Torymidae). Ann. Entomol. fenn., 48 : 33-36.

Annila E.,1984. Population fluctuation of some cone and seed insects in Norway spruce, in : Proceedings of Cone and Seed Insects Working party Conference. International Union of Forestry research Organizations, July31-August 6, 1983 (H.O. Yates, ed.). Southeastern Forest Experiment Station, Athens, U.S.A. : 57-84.

Bakke A., 1963. Studies of the spruce cone insects Laspeyresia strobilella (L.) (Lepidoptera, Tortricidae), Kaltenbachiola strobi (Winn.) (Diptera, Itonidae) and their parasites (Hymenoptera) in Norway. Medd. Norsk. Skogforsoksv., 19 : 1-151.

Bakke A., 1971. Distribution of prolonged diapausing larvae in populations of Laspeyresia strobilella L. (Lep. Tortricidae) from spruce cones. Nor. Entomol. Tidsskr., 18 : 89-93.

Dickmann D.I. and T.T. Kozlowski, 1969 . Seasonal variations of reserve and structural components of Pinus resinosa cones. Am. J. Bot., 56 : 515 -520.

Ebell L.F., 1971. Girdling : its effect on carbohydrate status and on reproductive bud and cone development of Douglas-Fir. Can. J. Bot., 49 : 453-466.

Ebell L.F., 1972. Cone-Production and Stem-Growth response of Douglas-Fir to Rate and Frequency of Nitrogen Fertilization. Can. J. For. Res., 2 : 327-338.

Eis S., 1973. Cone pr duction in Douglas-Fir and grand Fir and its climatic requirements. Can. J. For. Res., 3 : 61-70.

Fabre J.P., 1986. Dynamique d· · populations de Megastigmus suspectus Var. pinsapinis Hoff. (Hyménoptère, Tortricidae) dans les Cédraies du Sud-Est de la france. In : Proceedings of the 2nd International Conference, Cone and Seed Insects Working Party IUFRO S2.07-01., Briançon (3-5 septembre 1986), A. Roques (Ed.) INRA Versailles : 127-145.

Fenner M., 1985. Seed Ecology. Chapman and Hall (Ed.), London. 151 pp.

Geri and F.Goussard. 1988. Régulation du cycle biologique de Diprion pini L. (Hyménoptère, Diprionidae) par la diapause. Incidence de la photophase et de la température. Z. angew. Entomol., (in press).

Grebenshchikova V.P. and F.V. Naumov, 1985. Ecological features of Diptera in communities of Cone-Inhabiting Insects. In : Skarlato, O.A. (Ed.) Systematics of Diptera (Insect). Ecological and Morphological Principles. New Delhi, Oxonian Press: 18-22.

Hedlin A.F., G.E. Miller and D.A. Ruth, 1982. Induction of prolonged diapause in Barabara colfaxiana (lepidoptera : Olethreutidae) : Correlations with cone crops and weather. Can. Entomol., 114 : 465-471.

Hussey N.W., 1955. The life-histories of Megastigmus spermotrophus Wachtl. (Hym. Chalcidoidea) and its principal parasite, with descriptions of the developmental stages. Trans. R. Entomol. Sc. London., 106, (2) : 133-151.

Hussey N.W., 1956. The extent of seed-loss in Douglas-Fir caused by Megastigmus. Scots. For., 10 : 191-197.

Janzen D.H., 1971. Seed predation by animals. Ann. Rev. Ecol. Syst., 2 : 465-92.

Lessman D., 1974. Ein Beitrag zur Verbreitung und Lebensweise von Megastigmus spermotrophus Wachtl. und Megastigmus bipunctatus Swed. Z. angew. Entomol., 75 : 1-42.

Lowry W.P., 1966. Apparent meteorological requirements for abundant cone crops in Douglas-Fir. Forest Sci., 12 : 185-192.

Mattson W.J., 1972. The role of insects in the dynamics of cone production of red pine. Pinus resinosa. Thesis. Univ. Minnesota., 158 p.

Mattson W.J., 1978. The role of insects in the dynamics of cone production of red pine. Oecologia., 33 : 327-339.

Miller G.E. and A.F. Hedlin, 1984. Douglas-Fir cone moth and cone gall midge : Relation of damage and prolonged diapause to seed cone abundance in British Columbia. In : Proceedings of the Cone and Seed Insects Working Party Conference, International Union of Forestry Research Organizations, July 31-August 6, 1983, Athens (H.O.Yates III, ed.), Southeastern Forest Experiment Station, Athens, U.S.A. : 91-99 pp.

Miller G.E. and D.S. Ruth, 1986. Effect of temperature during May to August on termination of prolonged diapause in the Douglas-Fir cone moth (Lepidoptera : Tortricidae). Can. Entomol. : 1073-1074.

Nesin A.P., 1984. To the knowledge of diapause of some pests of the cones and seeds of the conifers. Rev. Entomol. U.R.S.S., 63, (2) : 225-230.

Roques A., 1981. Biologie et répartition de Megastigmus spermotrophus Wachtl. (Hymenoptera. Chalcidoidea. Torymidae) et des autres insectes liés aux cônes dans les peuplements forestiers et vergers à graines français du sapin de Douglas. Pseudotsuga menziesii (Mirb.) Franco. Acta Oecol. Oecol. Applic., 2, 2. 131-138.

Roques A., 1983. Les insectes ravageurs des cônes et graines de conifères en France. INRA - 135 pp.

Roques A. and J.P.Raimbault, 1986. Cycle biologique et répartition de Megastigmus wachtli (Stein) (Hymenoptera, Torymidae), chalcidien ravageur des graines de cyprès dans le Bassin méditerranéen. Z. Ang. Entomol., 101, 370-381.

Roques A., 1988. The Larch cone fly in the French Alps in A.A. BERRYMAN (Ed) : "Population dynamics of forest insects". Washington, U.S.A., 1-28.(In press).

Roques A., 1986a. Dynamics and Forecast of Larch Cone Maggot Populations in the French Alps. In: Proceedings of the 2nd conference of the "Cone and Seed Insects" Working Party.IUFRO S2.07-01.(Briançon 3-5/9/1986), 167-178.

Roques A., 1986b. Dynamique d'infestation des nouveaux vergers à graines de Douglas du Sud de la France par le chalcidien ravageur Megastigmus spermotrophus Wachtl. (Hym. Torymidae). 18th IUFRO World Congress. September 7-16, 1986. Ljubljana, 685-694.

Stadnitskii G.W., G.I. Iurchenko, A.N. Smetanin, V.P. Grebenshchikova et M.V. Pribylova, 1978. (Cone and Seed Pests of Conifers) (In Russian). Moscou : Lesnaia promyshlennost., 198 p.

NATURAL ENEMIES OF CONE AND SEED INSECTS OF WORLD CONIFERS

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SUMMARY

Nine members of the Cone and Seed Insects Working Party have submitted information on published natural control agents of conifer cone and seed insects of the world. Submitted to date are 1,132 listings representing 9 orders of fauna or flora that attack cone and seed insects. Over 97% of the listings belong to the insect (Insecta) orders Hymenoptera and Diptera. After scientific names have been verified by taxonomists, the most promising natural control agents will be selected and priorities established for possible population enhancement or exchange between geographic regions.

Key words: Cone and seed insects, natural enemies, biological control

INTRODUCTION

At the second IUFRO Cone and Seed Insects Working Party (S2.07-01) International Conference at Briancon, France, in 1986, I reported on the biological control agents of cone and seed insect and mite pests of world conifers (Yates 1986a). This preliminary report summarized the responses submitted by five Working Party members representing Finland, Canada, Romania, Mexico, and the United States. The data set consisted of only 119 parasite or predator entries. It represented 82 species of natural enemies attacking 36 of the more important seed-destroying insects throughout the world.[1]

Because the working party received responses from only five volunteer sources, it was concluded that, if a comprehensive world list was to be produced, all sources of information would have to be consulted in a systematic manner.

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[1]While not true insects, a number of mite species are known to attack conifer cones and seeds. For simplicity, "insects" is used to refer to all arthropod seed and cone predators.

After the Briancon meeting, therefore, the Working Party project expanded its coverage to published papers on cone and seed insects and taxonomic indexes to insect species. Furthermore, the committee no longer relied on volunteer contributions, but expanded to include representatives from nine nations. Each of these representatives assumed responsibility to abstract the literature from specific regions of the world.

MATERIALS AND METHODS

Cooperators in this project are Dr. Malgorzata Skrzypczynska of Krakow, POLAND; Dr. Alain Roques of Olivet, FRANCE; Dr. Jean Turgeon of Sault St. Marie, CANADA; Dr. Nicholas J. Mills of Ascot, UNITED KINGDOM; Dr. Alf Bakke of As, NORWAY; DR. Ljubodrag Mihajlovic of Beograd, YUGOSLAVIA; Dr. Ismail Chaudhry of Peshawar, PAKISTAN; and Dr. Keiji Kanamitsu of Nagoya, JAPAN. Each cooperator is responsible for the cone and seed insect literature from a specific region of the world. This arrangement minimizes, but does not completely eliminate, duplicate reporting of references.

Only creatures described as obligatory feeders on cones and seeds in the checklist of cone and seed insect and mite species (Yates 1986b) are included in this project. Excluded are the many defoliators and shoot moths that are considered facultative cone and seed feeders. That is, those that feed on cones and seed on occasion; however, their primary feeding site is other than cones and seeds. Such species as the spruce budworm, Choristoneura fumiferana (Clemens), and the European pine shoot moth, Rhyacionia buoliana (Denis and Schiffermuller), in North America, and the defoliator Zeiraphera diniana Guenee, in Europe, are excluded.

Information submitted for inclusion in this listing includes the scientific name, order, and family of both the host insect and the natural enemy along with the reference source. Also included are any published synonyms, invalid combinations, misspellings, etc. of the natural enemy. The latter include only those names that appear in the cone and seed insect literature. Spaces are also provided for designating the natural enemy's role (A = parasite; R = predator; and P = pathogen), coded comments, and country of occurrence. Coded comments provide specific information on the status of the pest (e.g.,hyperparasite; egg, larval, or pupal parasite).

One data source that recently became readily available is the entire "Hopkins U.S. System" in the United States. This information was documented on individual forms that were scattered over the United States at various Forest Experiment Stations. Recently, this entire file was entered on a computer. Information now may be retrieved on numerous parasite and predator identifications that have never been published.

Upon receipt of listings from each cooperator, the data are entered on a computer using a program called Reflex: The Analyst.[2] This program is capable of organizing and sorting data from five fields at any one time as well as searching and sorting for any element from within any one field.

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[2]Software available from Borland/Analytica, Inc., 4585 Scotts Valley Drive, Scotts Valley, California 95066.

RESULTS

To date, seven of the nine cooperators have submitted host and natural enemy lists (Table 1). These total 1,132 individual listings belonging to 9 orders of fauna and flora. Predictably, the greatest number of listings belong to the orders Hymenoptera and Diptera of the class insecta.

The limited number of species and listings within the orders Ascomycetes (fungi), Nematoda (nematodes), Acari (mites), Lepidoptera (moths), Heteroptera (true bugs), and Neuroptera (nerve wings) strongly suggest their limited potential as natural control agents. In fact, the actual classification of some listed species as natural enemies is seriously questioned. For example, the one species in the order Lepidoptera is most likely a casual rearing mistakenly considered a parasite or predator.

Likewise, the limited number of listings in the order Acari (Table 2) indicates their limited natural control value. However, even though the numbers are small, the potential importance of members of this order could be significant under certain circumstances.

The listed Coleoptera (beetles) all belong to families known to be predaceous (Table 3). However, nearly all in these families are associated with bark beetles or feed on larvae under bark or within burrows of wood borers. The limited number of listings suggests either that they were collected from rearings and misidentified as cone and seed insect predators or that they have a limited potential as natural control agents.

In the order Diptera, only species in the family Tachinidae have been generally reported parasitizing cone and seed insects (Table 4). Members of this family are internal parasites of a wide range of insects but particularly the Lepidoptera. To a lesser extent, they also parasitize insects in the orders Coleoptera, Hemiptera, and Hymenoptera (Stone et al. 1965).

Most of the Lonchaeidae are secondary invaders on diseased or injured plant material and are not known to be parasites or predators. Their activity in diseased or injured plant material probably accounts for their association with cone and seed insects. Interestingly this family also includes the genus Earomyia, which contains species that are primary invaders of cones (McAlpine 1956).

Some Pallopteridae (bark beetle predators or plant feeders), Chamaemyiidae (scale, mealybug, and aphid predators), and Cecidomyiidae (inquilines and predators) are predaceous, but predation of cone and seed insects is seriously questioned.

Table 1.--Numbers of families, genera, species, and listings of natural enemies in taxonomic orders that are listed as attacking cone and seed insects of world conifers.

	Numbers			
Natural Enemy Order	Families	Genera	Species	Listings
Hymenoptera	20	166	300	1,044
Diptera	5	28	21	62
Coleoptera	4	7	7	13
Acari	2	2	3	3
Neuroptera	1	1	2	5
Ascomycetes	1	2	1	2
Heteroptera	1	1	1	1
Nematoda	1	1	-	1
Lepidoptera	1	1	1	1

Table 2.--Numbers of genera, species, and listings of natural enemies in families in the order Acari (mites) that are listed as attacking cone and seed insects of world conifers.

	Number		
Acari Families	Genera	Species	Listings
Acaridae	1	2	2
Pyemotidae	1	1	1

Table 3.--Numbers of genera, species, and listings of natural enemies in families in the order Coleoptera (beetles) that are listed as attacking cone and seed insects of world conifers.

Coleoptera Families	Number		
	Genera	Species	Listings
Cleridae	3	4	6
Cantharidae	2	2	2
Melyridae	1	1	4
Dasytidae	1	1	1

Table 4.--Numbers of genera, species, and listings of natural enemies in families in the order Diptera (flies) that are listed as attacking cone and seed insects of world conifers.

Diptera Families	Numbers		
	Genera	Species	Listings
Tachinidae	22	17	53
Lonchaeidae	3	3	7
Pallopteridae	1	1	1
Cecidomyiidae	1	0	3
Chamaemyiidae	1	0	1
Totals	28	21	65

The order Hymenoptera represents over 91% of the natural enemy listings. Of these, nearly two-thirds (64.6%) are members of the families Braconidae (341) and Ichneumonidae (318). Members of both families are nearly all parasites and are particularly important parasites of the Lepidoptera (Krombein et al. 1979).

Table 5.--Numbers of genera, species, and listings of natural enemies in families in the order Hymenoptera (ichneumons, chalcids, ants, wasps, and bees) that are listed as attacking cone and seed insects of world conifers.

Hymenoptera Families	Number		
	Genera	Species	Listings
Braconidae	36	42	341
Ichneumonidae	50	128	318
Pteromalidae	25	44	131
Eulophidae	13	26	92
Torymidae	4	6	47
Platygastridae	3	7	24
Eupelmidae	2	8	23
Eurytomidae	2	7	16
Chalcididae	10	8	11
Encrytidae	8	6	10
Ceraphronidae	1	4	7
Trichogrammatidae	1	3	6
Figitidae	3	2	5
Calliceratidae	1	3	4
Bethylidae	1	2	3
Cynipidae	2	1	2
Eumenidae	1	1	1
Proctotrupidae	1	0	1
Scelionidae	1	1	1
Sphecidae	1	1	1

The status of members of the families Eumenidae, Cynipidae, Calliceratidae, Figitidae, and Ceraphronidae as cone and seed insect natural enemies is questioned. Many members of the family Sphecidae are important insect predators. The remaining Hymenoptera families (Pteromalidae, Eulophidae, Torymidae, Platygastridae, Eupelmidae, Eurytomidae, Chalcididae, Encyrtidae, Trichogrammatidae, Bethylidae, Proctotrupidae, and Scelionidae) are known parasites.

DISCUSSION

Past research on the use of natural enemies against cone and seed insects and mites is limited. Practically no research has been done on the possibility of using natural enemies against cone and seed pests because the biologies of natural enemies are incompletely known. Most of the published information on natural enemies has been the reporting of natural enemy species and their relative abundance found while collecting cone and seed pests.

Attempts have been made to utilize Trichogramma sp. (Hymenoptera: Trichogrammatidae) in Russia. From tests of pathogens for control of Lepidoptera cone feeders, it was concluded that the possibilities of effective use of these natural controls are quite limited (Stadnitskii et al. 1978; Fogal 1986; Fogal et al. 1986).

After this list of natural control agents is completed and the species names are verified, it will be published by contributing members of the Cone and Seed Insects Working Party. The currently accepted binomen of natural enemies will be listed by host. A second, phylogenetic listing will include currently accepted binomen of the natural enemies, followed by synonyms, misspellings, invalid combinations, etc., and their source references. The finished document will provide a ready reference by both host and natural enemy of all the known natural control agents of conifer cone and seed pests.

From these lists the most promising natural control agents will be selected for further biological study and their suitability for population enhancement or introduction into other geographic regions will be determined. Selection criteria will include relative abundance, fecundity, and host cone and seed pests.

ACKNOWLEDGMENTS

This paper is a preliminary summary of the hundreds of cone and seed insect natural enemy scientific names submitted by the Cone and Seed Insects Working Party project cooperators from around the world. Contributors include: M. Sprzypczynska, Poland; A. Bakke, Norway; N. Mills, Great Britain; A. Roques, France; L. Mihajlovic, Yugoslavia; and J. Turgeon, Canada. I also recognize the long hours of tedious and careful work of entering this data into a computer file by Ms. Pam Lowe and Mrs. Jo Hughey with the USDA Forest Service at Athens, Georgia, USA.

LITERATURE CITED

Fogal, W. H.
1986. Applying Beauveria Bassiana (Bals.) Vuill to soil for control of the spruce cone maggot Lasiomma Anthracina (Czerny). In Proceedings: 2nd Conference of the Cone and Seed Insects Working Party S2.07-01, p. 257-266. A. Roques ed. Inst. Natural de la Recherche Agronomique [Sta. de Zool. Forest. Olivet, France 1986].

Fogal, W. H., G. S. Thurston, and G. D. Chant.
1986. Reducing seed losses to insects by treating white spruce conelets with conidiospores of Beauvaria bassiana. Proc. Entomol. Soc. Ont. 117 (In Press).

Krombein, K. V., P. D. Hurd, Jr., D. R. Smith and B. D. Burks.
1979. Catalog of Hymenoptera in America north of Mexico. Vol. 1, Smithsonian Institution Press, Washington, D.C. 1198 pp.

McAlpine, J. F.
1956. Cone-infesting lonchaeids of the genus Earomyia Zett., with descriptions of five new species from western North America (Diptera: Lonchaeidae). Can. Entomol. 88: 178-196.

Stadnitskii, G. V., G. I. Iurchenko, A. N. Smetanin, V. P. Grebenshchikova, and M. V. Pribylova.
1978. Conifer cone and seed pests. "Lesnaia Promyshlennost" Publ. House. 168 pp.

Stone, A., C. W. Sabrosky, W. W. Worth, R. H. Foote, and J. R. Coulson.
1965. A catalog of the Diptera of America north of Mexico. Agr. Res. Serv. U.S.D.A Agr. Handb. 276. 1696 pp.

Yates, H. O., III
1986(a). Biological control agents of cone and seed insect and mite pests of world conifers. In Proceedings: 2nd Conference of the Cone and Seed Insects Working Party S2.07-01, p. 15-25. A. Roques ed. Inst. Natural de la Recherche Agronomique [Sta. de Zool. Forest. Olivet, France 1986].

Yates, H. O., III
1986(b). Checklist of insect and mite species attacking cones and seeds of world conifers. J. Entomol. Sci. 21: 142-168.

PROLONGED DIAPAUSE: THEORY AND OBSERVATIONS

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SUMMARY

Two kinds of density-independent prolonged diapause are conspicuously common in seed and cone insects. In predictive diapause the diapausing individual uses external signals to coincide its emergence with a large cone crop. In risk-spreading diapause a breeding female produces a mixture of offspring with varying diapause length to decrease variance in fitness. Prolonged diapause in many seed and cone insects seems to be a mixture of predictive and risk-spreading diapause. Coexistence of several species using the same host tree is facilitated by risk-spreading prolonged diapause, which buffers population size against poor years. Prolonged diapause plays an important role in many host-parasitoid systems involving seed and cone insects, but this field has remained largely unexplored.

Keywords: seed and cone insect, prolonged diapause, predictive diapause, risk-spreading diapause, variability, competition, host-parasitoid interaction.

INTRODUCTION

It is a common notion in population and evolutionary ecology that individuals have two basic options in escaping unfavourable environmental conditions: they may "escape in space" by dispersal, or they may "escape in time" by dormancy (Southwood 1977). Which option gives higher fitness, and should therefore be selected, depends both on the organism and the environment. Birds feeding on conifer seeds are constrained to opt for dispersal, or to use some alternative food source when the local cone crop fails (Smith and Balda 1979). Some seed and cone insects may use dispersal, but generally the temporal variation in cone production is well correlated within the dispersal radius of insects, and extra long diapause may be the only alternative for specialist seed and cone insects (for a contrast between specialist and generalist seed and cone insects see Roques this volume).

In extra long diapause (ELD), some individuals in the population remain in diapause longer than others and thereby miss one or more potential breeding opportunities (Hanski 1988). ELD may be achieved either by entering diapause earlier than others (premature diapause) or by terminating diapause later than others (prolonged diapause). In both cases, diapause induction may be density-independent or density-dependent. Hanski (1988) gives examples of the four kinds of ELD with reference to the relevant theoretical studies. Most of the theoretical work has focused on density-independent prolonged diapause, which is the kind of ELD used by seed and cone insects. Section 2 will outline the basic connection between temporal variability in fitness and ELD. In Section 3 I discuss competition between two or more species using the same resource, and how ELD may affect the outcome of such competition. A largely unexplored but interesting topic is ELD in coupled host-parasitoid systems (Section 4). Seed and cone insects provide interesting examples and challenges for futher work on ELD.

TEMPORAL VARIABILITY AND PROLONGED DIAPAUSE

A major problem facing most seed and cone insects is more or less unpredictably varying resource availability from one year to another (Hedlin 1964, Bakke 1971, Smith and Balda 1979, Fenner 1985). Prolonged rather than premature diapause is an effective solution to multiannual variation in resource availability, and prolonged diapause is universally observed in seed and cone insects. Seed predation by insects may be an ultimate cause of multiannual variation in cone production in many conifers (Janzen 1971, Smith and Balda 1979 and references therein), but the proximate causes are likely to be different. Therefore, insect population size in year t is a poor predictor of cone production in year $t+1$, and one could expect the seed and cone insects to have density-independent prolonged diapause, in other words that the induction of prolonged diapause is not affected by e.g. larval competition in seeds or cones. Bakke's (1971) observations on Cydia (Laspeyresia) strobilella (L.) in Norway support this prediction (see also Roques this volume).

Another useful classification is based on the function of ELD. In plants, a major reason for delayed germination of seeds is simply lack of suitable conditions for germination. A seed, once dispersed from the parent plant, cannot move voluntarily to locate a favourable germination site. If a seed is buried at a depth or at a site where germination would fail, it is better to stay dormant and wait for the chance event, e.g. soil disturbance, that would bring it to a suitable germination microhabitat. Grubb (1988) has coined the term disturbance-broken dormancy for such cases. Disturbance-broken dormancy is non-existent or very rare in insects (Hanski 1988), probably because the mobility of insects allows them to find favourable sites for development and reproduction (a possible example is insects inhabiting temporary pools; eggs may be forced to enter ELD if the pool dries up).

The two other kinds of dormancy in Grubb's (1988) classification are well represented in seed and cone insects, which probably all have diapause rather than simple quiescence (Danks 1987). In weather-dependent dormancy the diapausing individual waits for an appropriate environmental signal representing favourable conditions in some predictable time in the future. In seed and cone insects, the favourable situation would be a large cone crop in the following year. Perhaps a more appropriate term than weather-dependent diapause would be predictive diapause. Predictive diapause contrasts with the third functional type of prolonged diapause, risk-spreading diapause, in which a breeding female produces a mixture of offspring with different lengths of diapause; one expects that the mixture evolves to a value that maximizes the fitness of the breeding female. If diapause determination is density-independent, as is likely to be the case in seed and cone insects, we would expect all females to produce the same mixture of ELD and non-ELD offspring.

It is important to notice one fundamental difference between predictive and risk-spreading diapause: in the latter, the target individual whose fitness is affected by varying the length of the diapause is the breeding female; none of its diapausing offspring can individually "spread the risk" (before their own reproduction and through their own offspring). In contrast, the target individual in predictive diapause is the diapausing individual itself, though naturally it is also in the interest of a breeding female that its offspring make good decisions about terminating the diapause.

Annila's (1981) work on the seed and cone insects of the Norway spruce Picea abies in Finland provides an interesting example, in which different species using the same host tree show radically different diapause behaviours. Two cone insects C. strobilella and Strobilomyia (Lasiomma) anthracinum (Czerny) mostly emerged after one winter, but two seed insects Plemeliella abietina Seitner and Megastigmus strobilobius Ratzeburg always stayed in diapause for 2 to 4 years, most individuals emerging in 3 years. The cone production of the Norway spruce in Fennoscandia varies greatly from one year to another, but the variance in cone production has also a clear 3-year cyclic component (Hagner 1965, see analysis in Hanski 1988). It is tempting to suggest that different species with different diapause behaviours are tracking different components of temporal variation in cone production: the two cone insects track the irregular year-to-year variation, whilst the emergence of the two seed insects appears to be timed to coincide with the peak years of cone production. The cone insects have risk-spreading prolonged diapause, but the seed insects appear to have predictive prolonged diapause. An alternative explanation for the seed insects is that their diapause length has become fixed to an average of 3 years, corresponding to the long-term average of the cone crop cycle, whilst variation around this mean would represent risk-spreading diapause. Annila's (1981) results do not give unequivocal support to either hypothesis.

Predictive diapause

Observations showing that the seed and cone insects tend to emerge in years when the cone crop is largest indicate predictive diapause. Many such observations have been published (Bakke 1963, Stadnitskii et al. 1978, Annila 1981, Hedlin et al. 1982), but in other cases no correlation has been found (Hedlin 1964, Annila 1981), suggesting risk-spreading diapause. The two functions of diapause may of course be present together in many seed and cone insects. The diapausing individual itself should always aim at predictive diapause, because it cannot increase its own reproductive success through (mother's) risk-spreading diapause.

The most likely signal that the insects may use in timing their emergence is the critical temperature for cone development in the year before emergence (Annila 1981, Hedlin et al. 1982). It should be possible to conduct controlled experiments to further elucidate this question. In the initiation of prolonged diapause, it is possible that chemical changes in the host tree associated with varying levels of cone production in the following year may play an important role (see Roques this volume for a discussion). An example of predictive diapause in species other than seed and cone insects is reported by Powell (1974), who found that the moth Ethmia semilugens (Zeller) emerged, after spending 33 months in diapause, only 40 days following artificial watering. The species inhabits desert margins and other arid places in North America, and appears to time its emergence to coincide with germination of its annual host plants, which themselves are likely to have predictive dormancy.

Risk-spreading diapause

Cohen's (1966, 1968) studies on delayed germination of seeds pioneered the study of risk-spreading, density-independent prolonged diapause. Cohen (1966) used a density-independent population model, and he assumed that the environment is always in one of two states, good or bad, the two states occurring in a random sequence. Cohen solved for the optimal fraction of individuals emerging from (prolonged) diapause (Q) by maximizing the geometric mean growth rate, obtaining

$$Q = (pW-S)/(W-S),$$

where p is the probability that the environment is good, W is a factor by which breeding individuals multiply in a good year, and S is the proportion of individuals in (prolonged) diapause surviving from one year to another. Cohen assumed that breeding would fail entirely in bad years. Cohen's result predicts that the optimal fraction of individuals emerging should approximately equal the probability of a good year (especially for large W).

More recent theoretical contributions include studies in which dispersal and prolonged diapause are assumed to be two alternatives for the insect (MacArthur 1972, Venable and Lawlor 1980, Bulmer 1984, Klinkhamer et al. 1987), and models based on density-dependent population dynamics (Bulmer 1984, Levin et al. 1984, Ellner 1985a,b). The main results of these studies may be summarized as follows:

1) In agreement with Cohen's result, the greater the variance in the favourability of breeding seasons, the greater the frequency of prolonged diapause (Bulmer 1984). Annila (1982) compared two species of Megastigmus breeding in the seeds of the Siberian Fir Abies sibirica (M. specularis Walley) and the Douglas Fir Pseudostuga menziesii (M. spermotrophus Wachtl) in Finland. The Siberian Fir has relatively stable cone crops in comparison with the Douglas Fir, and in agreement with the theoretical prediction, Annila (1982) found that while M. specularis mostly emerged after one winter, without prolonged diapause, the Douglas Fir seed predator M. spermotrophus mostly emerged after three to five years. For a more thorough analysis of prolonged diapause in the European Megastigmus see Roques (this volume). It would be interesting to know whether variation in the diapause behaviour between localities (e.g. Bakke 1971) can generally be attributed to differences in resource variability, as suggested by an example reported by Roques (this volume: M. wachtli in two contrasting localities in France).

What really matters in the determination of prolonged diapause is not year-to-year variability in the favourability of breeding seasons as such but variation in the breeding success of individuals emerging in different years. When such variation is high, risk-spreading prolonged diapause is selected for, regardless of the cause of variation (Bulmer 1984, Hanski 1988). Prolonged diapause may be selected for even in a constant environment if there are cyclic or chaotic changes in the population size due to e.g. severe competition. This may be an important consideration for seed and cone insects with often intense competition within and between species (Mattson 1980, 1986, Annila 1982, Miller and Hedlin 1984).

2) In contrast to Cohen's result, which was based (unrealistically) on a density-independent population model, the tendency towards prolonged diapause is greatly increased by high survival in diapause. Unfortunately, there are little data for survival in prolonged diapause in seed and cone insects (but see Roques this volume).

3) Dispersal between more or less independently varying environments is an alternative means to prolonged diapause of "spreading the risk". Dispersal could be expected in species with poorly synchronized temporal variation in cone production between individual trees. Insect species with high dispersal ability could also be expected to show less prolonged diapause than species with poor dispersal ability. The cone insects in Annila's (1981) study (above) are larger and hence probably better dispersers than are the seed insects, which may contribute to the lower frequency of prolonged diapause in the former.

COMPETITION AND PROLONGED DIAPAUSE

Yates (1986) lists more than 360 species of insects reared from conifer seeds and cones, and generally many species use the same host species (Bakke 1963, Annila 1981, Skrzypczynska 1984). Taking into account that competition is well documented for many seed and cone insect assemblages (Annila 1973, Smith and Balda 1979, Mattson 1986, Rappaport and Volney this volume), one may ask how coexistence of many species on the same resource is possible.

One possible explanation is based on the great temporal variation in the size of cone crops in many conifers. An apparent exception confirming the rule is the lodgepole pine, which has a relatively stable cone crop size and very few seed and cone predators (Smith and Balda 1979), though it may be difficult to discount the possibility that the well-developed structural defenses in the lodgepole pine are the cause of low diversity of its seed and cone predators.

To further develop the hypothesis that variation in cone crop size facilitates coexistence, let us take an example of two species, of which one is a superior competitor and would outcompete the second species in a constant environment. Let us assume that there is stochastic variation in the cone crop size between years, and let us assume that, as a response to such variation, the insect species have risk-spreading, density-independent prolonged diapause. In this situation, the inferior species may survive in spite of competition if its probability of survival in prolonged diapause is greater than that of the superior species, and especially if its population growth rate is also higher. High growth rate allows the inferior competitor to take advantage of the peak years of cone production, when competition is temporarily ameliorated by increased resource availability, and high survival in prolonged diapause allows the inferior species to "store" the benefit of the peak years for several poor years. This is a particular example of the general non-equilibrium model of competition developed by Chesson (1983, 1986, Chesson and Huntly 1988). Unfortunately, I have not found suitable data for guilds of seed and cone insects to test whether inferior competitors are likely to survive because of low mortality in diapause and/or high population growth rate, e.g. high fecundity.

Interspecific competition may also affect the type of prolonged diapause adopted by the insect. Hanski (1988) has discussed the example of the four common species of seed and cone insects breeding in the Norway Spruce in Finland (previous Section). The two seed insects P. abietina and M. strobilobius are inferior in competition to the cone insects C. strobilella and H. anthracinum (Annila 1981). Given that the cone insects have adopted a risk-spreading diapause allowing them to track the year-to-year variation in cone production, the seed insects may do best by adopting predictive prolonged diapause and "specializing" in the years of exceptionally high cone production. Hanski (1988) has demonstrated, with a mathematical model, that the two kinds of

species can coexist in spite of asymmetric competition, if the regular, cyclic component in cone production is sufficiently strong and the mortality of diapausing individuals is not too high. This model does not assume any differences in species' growth rates or survival rates in diapause.

The Douglas Fir in North America (Hedlin 1964, Volney 1984) and the Norway Spruce in northern Europe (Annila 1981) support insect assemblages with striking taxonomic similarity: both host trees have typically an abundant tortricid, an abundant cecidomyid and an abundant torymid. The main difference is that while the Norway Spruce has an abundant anthomyiid (Strobilomyia anthracinum) the Douglas Fir has typically an abundant pyralid (Dioryctria sp.). Such family-level similarity in the species composition of seed and cone insects suggests a non-random structure of the community, probably molded by interspecific competition, for which there is good evidence (Norway Spruce: Annila 1973; Douglas Fir: Rappaport and Volney this volume and references therein). Coexistence of many congeners with similar biologies would probably be more difficult than coexistence of distantly related taxa, though there are guilds of congeneric seed and cone insects using the same host plant in the same place (e.g. Roques et al. 1983).

HOST-PARASITOID DYNAMICS AND PROLONGED DIAPAUSE

Seed and cone insects are often attacked by many species of parasitoids (Bakke 1963, Stadnitskii et al. 1978), and both the host and the parasitoid will have prolonged diapause (e.g. Annila 1981). Prolonged diapause may greatly complicate the dynamics of such three-level systems, where the dynamics of the host are affected by the externally imposed fluctuations in resource availability plus the coupled host-parasitoid interaction. All three trophic levels, the host tree, the cone insect and its parasitoid, are engaged in a struggle to desynchronize their temporal dynamics with the consumer but to synchronize their dynamics with the resource.

I am not aware of any theoretical studies dealing with all three trophic levels or even modelling just the host-parasitoid dynamics with prolonged diapause in both species. In Annila's (1981) work on the seed and cone insects of the Norway spruce, the parasitoids appeared to stay longer in prolonged diapause than the host species, but whether this is a general pattern and whether it is adaptive for the parasitoid remain open questions.

Another point worth making in this context is that if the host-parasitoid dynamics are cyclic or chaotic, prolonged diapause could be selected for in the host population even in the absence of fluctuations in resource availability (Hanski 1988). I have pointed out above that prolonged diapause is a response to temporal variation in breeding success, and it does not matter whether the cause of such variation is externally imposed resource

fluctuation, species own unstable dynamics (intraspecific competition), or unstable host-parasitoid dynamics. Seed and cone insects are an extreme example in which all three sources of variability are often present - it is no wonder that prolonged diapause is conspicuously common in them. The large variety of seed and cone insects living under varying environmental conditions provide a rich material for an ecologist interested in ELD, and one may hope that studies on the biological basis of prolonged diapause could help the entomologist engaged in solving the practical problems caused by seed and cone insects.

LITERATURE CITED

Annila, E., 1973: Chemical control of spruce cone insects in seed orchards. Commun. Inst. For. Fenn. 78:1-25.

Annila, E., 1981: Fluctuations in cone and seed insect populations in Norway spruce. (In Finnish with English summary.) Commun. Inst. For. Fenn. 101:1-32.

Annila, E., 1982: Diapause and population fluctuations in Megastigmus specularis Walley and Megastigmus spermotrophus Wachtl. (Hymenoptera, Torymidae). Ann. Ent. Fenn. 48:33-36.

Bakke, A., 1963: Studies on the spruce-cone insects Laspeyresia strobilella (L.) (Lepidoptera: Tortricidae), Kaltenbachiola strobi (Winn.) (Diptera: Itonidae) and the parasites (Hymenoptera) in Norway. Meddel. Norske Skogforsoskvesen 19:1-151.

Bakke, A., 1971: Distribution of prolonged diapausing larvae in populations of Laspeyresia strobilella L. (Lep. Tortricidae) from spruce cones. Norsk Ent. Tidsskr. 18:89-93.

Bulmer, M. G., 1984: Delayed germination of seeds: Cohen's model revisited. Theor. Pop. Biol. 26:367-377.

Chesson, P. L., 1983: Coexistence of competitors in a stochastic environment: the storage effect. In: H.I. Freedman and C. Strobeck (eds.), Population biology. Lecture Notes in Biomathematics 52:188-198.

Chesson, P. L., 1986: Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theor. Pop. Biol. 28:263-287.

Chesson, P. L., and N. Huntly, 1988: Community consequences of life-history traits in a variable environment. Ann. Zool. Fennici 25:5-16.

Cohen, D., 1966: Optimizing reproduction in a randomly varying environment. J. Theor. Biol. 12:119-129.

Cohen, D., 1968: A general model of optimal reproduction in a randomly varying environment. J. Ecol. 56:219-228.

Danks, H. V., 1987: Insect dormancy: an ecological perspective. Biological Survey of Canada No. 1, Ottawa.

Ellner, S., 1985a: ESS germination strategies in randomly varying environments. I. Logistic-type models. Theor. Pop. Biol. 28:50-79.

Ellner, S., 1985b: ESS germination strategies in randomly varying environments. II. Reciprocal-yield laws. Theor. Pop. Biol. 28:80-116.

Fenner, M., 1985: Seed ecology. Chapman and Hall, London.

Grubb, P. J., 1988: The uncoupling of disturbance and recruitment, two kinds of seed bank, and persistence of plant populations at the regional and local scales. Ann. Zool. Fennici 25:23-36.

Hagner, S., 1965: Cone crop fluctuations in Scots Pine and Norway Spruce. Studia Forest. Suec. 33:1-21.

Hanski, I., 1988: Four kinds of extra long diapause and population dynamics in insects. Ann. Zool. Fennici 25:37-54.

Hedlin, A. F., 1964: Results of a six-year plot study on Douglas-fir cone insect population fluctuations. For. Sci. 10:124-128.

Hedlin, A. F., G. E. Miller, and D. S. Ruth, 1982: Induction of prolonged diapause in Barbara colfaxiana (Lepidoptera: Olethreutidae): correlations with cone crops and weather. Can. Entomol. 114:465-471.

Janzen, D. H., 1971: Seed predation by animals. Ann. Rev. Ecol. Syst. 2:465-492.

Klinkhamer, P. G. L., T. J. de Jong, J. A. J. Metz, and J. Val, 1987: Life history tactics of annual organisms: the joint effects of dispersal and delayed germinatior Theor. Pop. Biol. 32:127-156.

Levin, S. A., D. Cohen, and A. Hastings, 1984: Dispersal strategies in patchy environments. Theor. Pop. Biol. 26:165-191.

MacArthur, R. H., 1972: Geographical Ecology. Harper & Row, New York.

Mattson, W. J., 1980: Cone resources and the ecology of the red pine cone beetle, Conophthorus resinosae (Coleoptera: Scolytidae). Ann. Entomol. Soc. Amer. 73:390-396.

Mattson, W. J., 1986: Competition for food between two principal cone insects of red pine, Pinus resinosa. Envir. Entomol. 15:88-92.

Miller, G. E, and A. F. Hedlin, 1984: Douglas-fir cone moth and cone gall midge: relation of damage and prolonged diapause to seed cone abundance in British Columbia, Canada. In: Yates III H.O. (ed.), Seed and cone insect Working Party S2.07-01, IUFRO. Asheville, North Carolina, USA.

Roques, A., J. P. Martinez, and A. Delplanque, 1983: Les dipt res Anthomyiidae du genre Lasiomma Stein. ravageurs des c nes et graines de mél ze d'Europe (Larix decidua Mill.) en France. I: Taxonomie et répartition. Z. Angew. Entomol. 95:429-439.

Skrzypczynska, M., 1984: Insects of cones and seeds of the European larch, Larix decidua Mill., and Polish larch, L. polonica Rac., in Poland. In: Yates III H.O. (ed.), Seed and cone insect Working Party S2.07-01, IUFRO. Asheville, North Carolina, USA.

Smith, C. C., and R. P. Balda, 1979: Competition among insects, birds and mammals for conifer seeds. Amer. Zool. 19:1065-1083.

Southwood, T. R. E., 1977: Habitat, the templet for ecological strategies? J. Anim. Ecol. 46:337-365.

Stadnitskii, G. V., G. I. Iurchenko, A. N. Smetanin, V. P. Grebenshchikova, and M. V. Pribylova, 1978: Conifer cone and seed pests. Moscow, Lesn. Prom-st. 168 pp.

Venable, D. L., and L. Lawlor, 1980: Delayed germination and dispersal in desert annuals: escape in space and time. Oecologia 46:272-282.

Volney, W. J. A., 1984: Competition and survival among insects colonizing Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) cones. In: Yates III H.O. (ed.), Seed and cone insect Working Party S2.07-01, IUFRO. Asheville, North Carolina, USA.

Yates III, H. O., 1986: Checklist of insect and mite species attacking cones and seeds of world conifers. J. Entomol. Sci. 21:142-168.

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DISTRIBUTION SPATIALE DE MEGASTIGMUS SUSPECTUS VAR. PINSAPINIS HOFF. (HYM. TORYMIDAE), SUR CEDRUS ATLANTICA MANETTI, DANS UN PEUPLEMENT DU SUD-EST DE LA FRANCE

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R E S U M E

Cette note traite de la distribution spatiale des cônes, de celle du nombre de graines/cône parasitées par Megastigmus suspectus Var. pinsapinis et de celle des autres catégories de graines. Dix cèdres de l'Atlas (Cedrus atlantica), d'environ 11,50 m de hauteur, fructifères, ont été choisis dans un peuplement du Massif du Ventoux (Vaucluse). Ils ont été divisés, verticalement en 11 strates de 1 m, horizontalement en 4 quadrants correspondants aux 4 secteurs géographiques. Sur chacune de ses parties, on a récolté un échantillon de cônes égal au dixième de la récolte. Ramené au laboratoire, le nombre des graines de chaque catégorie a été obtenu, pour chaque cône, après sa désarticulation, par un tri densimétrique et par un tri radiographique.

La distribution verticale du nombre de cône est en rapport direct avec la quantité de biomasse végétale (estimation visuelle). Entre 3 et 8 m se trouve 82 % de la récolte. Le nombre de graines parasitées par M. suspectus, de 7 graines par cône, correspond à une faible attaque et à une récolte abondante. La moyenne du nombre de graines parasitées/cône de chaque strate augmente nettement avec leur hauteur. De 0 à 6 m, les valeurs

sont significativement plus faibles que celles qui sont au-dessus de 7 m. La raison de ces différences devrait être recherchée dans le comportement de ponte des femelles de M. suspectus. La distribution verticale du nombre de graines saines/cône varie beaucoup d'un arbre à l'autre, mais en regroupant ces derniers en 3 catégories on trouve quelques différences significatives. Le nombre de graines saines/cône est toujours élevé dans la partie médiane du houppier. Les valeurs les plus faibles sont situées dans la partie basse des arbres et pour le groupe des plus fructifères, qui ont tendance a être dominants, dans la cime. Le nombre de graines vides/cône, de taille normale, est semblable sur les 11 strates, les différences entre les arbres étant trop élevées. Le nombre de graines vides/cône de petite taille est, au contraire, très important entre 0 et 1 m.

Le nombre de cônes sur le secteur nord est très faible, tout comme la biomasse végétale. Le nombre de graines parasitées/cône est plus élevé sur les secteurs nord et ouest qui offrent sans doute aux femelles de Megastigmus un effet "silhouette" plus marqué. Sur le secteur ouest, le nombre de graines saines/cône est plus faible. Enfin, le nombre de graines vides/cône, quelles que soient leur taille, est semblable sur tous les quadrants.

La détermination précise des taux d'attaques de M. suspectus tient compte de ces résultats. L'échantillon est composé de cônes récoltés sur les différentes strates du houppier. Les différences signalées entre les secteurs sont relativement moins importantes.

Mots clés : Insectes des cônes et des graines
Megastigmus suspectus Var. pinsapinis Hoff
Cedrus atlantica Mannetti
Distributions spatiales.

SUMMARY

SPATIAL DISTRIBUTION OF THE CEDAR SEED WASP, MEGASTIGMUS SUSPECTUS VAR. PINSAPINIS HOFF. (HYM. TORYMIDAE) IN A STAND OF SOUTH-EAST OF FRANCE.

This note deals about the spatial distribution of the cones and about the number of seeds/cone parasited by Megastigmus suspectus Var. pinsapinis and about that of other categories of seeds. Ten Atlas cedars - about 11.5 m high - with a good crop, have been selected among a stand from Montain Ventoux (Vaucluse). They have been divided in 11 different vertical levels of 1 m and in 4 horizontal quarters corresponding to the 4 geographical areas. On each parts, we have recolted one cone sample of one

tenth of the total number. In the laboratory, the number of seeds of each cone has been obtained by its desarticulation and by a densimetric and radiographic classifying.

The vertical distribution of the cone number is related to the quantity of vegetal biomass (visual estimation). Between 3 and 8 m, we find 82 % of the crop. The number of seeds parasited by M. suspectus - 7 seeds per cone - corresponds to a little attack and to an abondant crop. The average number of parasited seeds/cone increases with the high. From 0 to 6 m, the numbers are significatively lower those above 7 m. the reason of these differences should be researched in the ethology of the laying of the M. suspectus females. The vertical distribution of the number of good seeds varies a lot from one tree to another, but if we gather these last ones in three categories, we can find some significative differences. The number good seeds is always high in the middle part of the trees, the lowest numbers are situated in the low part of the trees and for the trees with a good crop - which are the highest - in the top. The number of empty seeds cone of normal size is the same on the 11 levels, the differences between the trees being too important. The number of empty seeds of small size is, on the contrary, very important between 0 and 1 m.

The number of cones on the northern side is very low like the vegetal biomass. The number of parasited seeds/cone is higher on the north and west sides which probably offer a more important "silhouette" effect to M. suspectus females. On the western side, the number of good seeds is lower. At last, the number of empty seeds, whatever their size are, is the same in all the quarters.

The exact determination of the attack rates of M. suspectus take this results into account. The sample composed of cones from different levels of the trees. The differents observed in the quarters are less important.

Key words : cone and seed insects
Megastigmus suspectus var. pinsapinis Hoff.
Cedrus atlantica Manetti
Spatial distributions

I - INTRODUCTION

Megastigmus suspectus, Var. pinsapinis, est un ravageur des graines du Cèdre de l'Atlas : Cedrus atlantica Manetti, dans le sud de la France. Il a été signalé pour la première fois en 1950 par Berland à Apt en Vaucluse. Dans une communication antérieure (FABRE, 1986), nous avons précisé les principales caractéristiques de sa biologie, l'importance de ses dégâts et l'influence de quelques facteurs sur la dynamique de ses populations.

Le cycle évolutif de ce Chalcidien semminiphage s'échelonne sur deux ans, il est en relation avec le développement de l'inflorescence femelle. Les fluctuations de ses populations sont très liées à celles de son hôte. Le taux de prolongement de la diapause et la mortalité larvaire interviennent en faveur d'une meilleure coïncidence entre le nombre de femelles aptes à pondre et le nombre des inflorescences femelles disponibles.

La présente note traite de la distribution spatiale des graines parasitées par M. suspectus et celle des autres catégories de graines du cône, sur le cèdre de l'Atlas.

II - MATERIEL ET METHODES

L'étude a été réalisée au Mont-Ventoux, dans un peuplement de la Forêt communale de Bédoin (Vaucluse), longitude 3,23 E, latitude 49,05 N, altitude 850 m. C'est une futaie régulière, assez ouverte, d'environ 30 ha, issue d'une plantation en potets, constituée en 1928 par l'Administration des Eaux et Forêts. Le peuplement est situé dans la partie basse de la série méditerranéenne du chêne pubescent (BARBERO et al., 1978) ; il a été classé pour la récolte des cônes. Dix arbres de 10 à 13 m de hauteur (moyenne 11,50 m) et de 85 à 146 cm de circonférence (moyenne 114 cm), porteur d'une récolte de 200 à 760 cônes (moyenne 411 cônes), ont été choisis le long d'un cheminement. On a retenu, des individus fructifères, qui avaient tendance a être dominants et isolés. Chaque arbre a été divisé, horizontalement en 4 quadrants ou secteurs correspondant aux 4 orientations géographiques et verticalement en 11 strates de 1 m, à partir du niveau du sol. Dans chacune de ces parties, ainsi délimitées et sur chaque arbre, on a récolté un échantillon constitué d'un nombre de cônes égal au dixième de la récolte.

Ramenés au laboratoire, les cônes sont désarticulés, les graines sont désailées et on sépare celles de petite taille de celles de taille

normale. Ces dernières sont soumises à un tri densimétrique dans de l'alcool éthylique à 99 % en volume. Les graines saines tombent alors au fond du récipient, les autres, qui surnagent, sont rangées sur un film de plastique transparent, collant, lui-même disposé au préalable sur un chassis métallique de 29 x 26 cm comportant 5 séparations longitudinales. L'ensemble est mis sur une plaque sensible (film Kodak "Industrex" de format 24 x 30 cm), placée pendant 30 secondes dans un appareil à rayons X (modèle "Sigma", 5 KV, Compagnie Générale de Radiologie) réglé sur 5 m A, 15 KV. Après développement du cliché, on identifie les graines parasitées contenant une larve de Megastigmus, les autres étant vides. Ces dernières sont en général des graines dont l'embryon ne s'est pas développé, mais certaines, que l'on ne peut pas séparer de cette façon, contiennent, par contre, une larve de Megastigmus qui est morte en cours de développement. Ainsi, le nombre de graines parasitées est situé entre les deux valeurs approchées suivantes : l'une, par défaut, correspond au nombre de graines contenant une larve vivante, identifiable sur la radiographie, l'autre par excès, est la valeur précédente augmentée du nombre de graines vides de taille normale.

Les effectifs, des différentes catégories de graines, obtenus de chaque cône sont ensuite regroupés par arbre, par secteur ou par quadrant. Les moyennes / cône sont calculées avec un intervalle de confiance au risque α = 0,05 %. Pour les graines parasitées, on a donné aussi les effectifs ramenés à un cône "standard" contenant 100 graines de grande taille. On a effectué des analyses de variance à un facteur sur les données individuelles, quelquefois après transformation normalisante. La normalité des différentes distributions a été jugée d'après la droite de "Henry" et les coefficients de "Pearson". Pour vérifier l'égalité des variances des moyennes on a utilisé le test de "Hartley", mais les effectifs n'étant pas constants, ce dernier ne donne que certains résultats (DAGNELIE, 1975). Les comparaisons multiples des moyennes des échantillons ont été faites à l'aide du test de "Duncan".

III - RESULTATS ET DISCUSSION

Nous avons examiné 411 cônes contenant 54063 graines, 41029 (76 %) d'entre elles avaient un embryon susceptible de se développer, 2766 (5 %) contenaient une larve vivante de M. suspectus, 5616 (10 %) étaient vides, 4652 (9 %) étaient incomplètement formées et de petite taille. Autrement dit, chaque cône contenait en moyenne 132$\pm$3 graines, dont 100$\pm$3 saines, 7$\pm$1 parasitées, 14$\pm$1 vides de taille normale, 11$\pm$1 vides de petite taille. Le taux d'attaques compris entre 6 et 18 % est donc relativement faible. Il correspond à une récolte importante (FABRE, 1986) qui a été estimée sur une autre parcelle de ce même peuplement à environ 10000 cônes par ha.

3.1. Comparaison des différents strates

31.1. Distribution des cônes

Le nombre de cônes dans chacune des 11 strates des 10 arbres varie de 50, entre 10 et 11 m, à 680, entre 4 et 5 m (tab. 1). Le nombre de cônes strate est d'abord faible au-dessus du niveau du sol jusqu'à 1 m, il augmente ensuite jusqu'à 4 m, le maximum étant atteint entre 4 et 7 m, au-dessus il diminue à nouveau pour atteindre une valeur très faible dans la cime des arbres entre 10 et 11 m. Ces variations sont en relation avec l'abondance de la biomasse végétale, ce qui n'est pas une surprise. Le maximum de la biomasse végétale (estimation visuelle) se situe entre 3 et 8 m, là où se trouve 82 % de la récolte. Les branches basses sont relativement développées, les arbres ayant tendance a être isolés, mais elles reçoivent moins de lumière et sont en compétition, soit avec le sous-bois, soit avec de plus jeunes arbres. Les cimes, comme sur tous les jeunes cèdres de l'Atlas, sont très réduites. TOTH en 1978 avait déjà signalé, au Ventoux, une plus faible production de cônes dans le tiers inférieur des arbres.

31.2. Distribution des graines parasitées

Le nombre moyen de graines parasitées/cône, de (7±1), varie de 2±3, entre 0 et 1 m, à 12±5, entre 9 et 10 m (tab. 2). Ces résultats exprimés par rapport à un cône "standard" de 100 graines de grande taille sont pratiquement semblables (fig. 1). Le taux moyen de graines parasitées/cône, de 9±2 %, varie alors de 3±1 %, entre 2 et 3 m, à 11±5 %, entre 9 et 10 m. Dans les deux cas, les intervalles de confiance sont plus élevés entre 0 et 1 m et entre 9 et 11 m. La variabilité du nombre des graines parasitées entre les cônes est plus importante sur les premières branches et vers la cime. L'analyse de la variance du nombre de graines parasitées/cône, après transformation Log (x+1) montre que les différences entre les strates sont supérieures aux différences entre les cônes, toutes strates confondues, F (5,00) étant très hautement significatif (F = 2,32 avec α = 0,005 et avec 10 et 400 dl). L'hypothèse nulle de l'égalité du nombre de graines parasitées/cône des différentes strates est donc à rejeter. On donne sur le tableau 3 le classement de ces moyennes par ordre décroissant. Au seuil de 5 %, elles forment deux populations significativement différentes, la première de 0 à 6 m, la seconde au-dessus de 7 m.

Sur les 10 arbres du peuplement du Ventoux, le nombre de graines

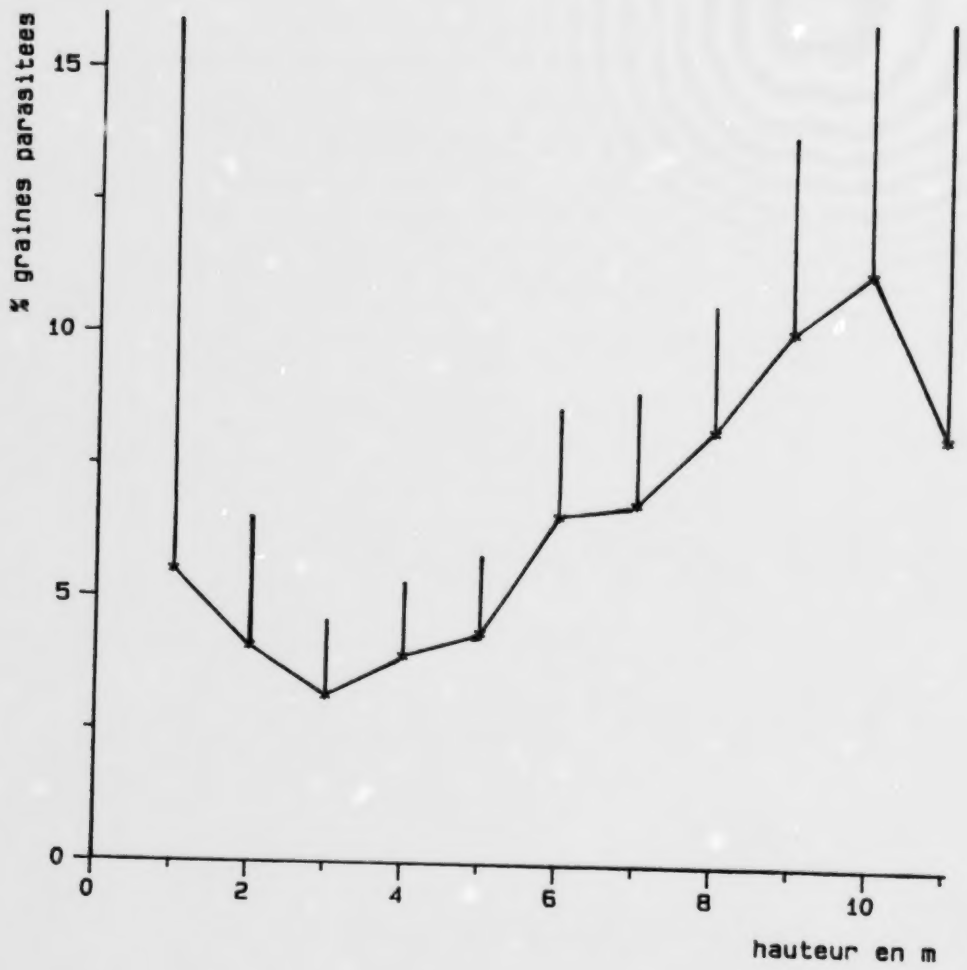

Figure 1 : Pourcentages moyens par cône de graines parasitées et intervalles de confiance, sur les différents strates des 10 cèdres de l'Atlas du peuplement du Mont Ventoux.

Average percentages of parasited seeds per cone and confidence intervals on the different levels on 10 Atlas cedars of a stand of Ventoux Montain.

Tableau 1 : Distribution verticale des cônes sur 10 cèdres du peuplement du Mont Ventoux.

Cones vertical distribution of 10 cedars stand of Ventoux Montain.

Hauteur en m	Nombre de cônes	%
0 - 1	70	1,7
1 - 2	210	5,1
2 - 3	430	10,5
3 - 4	490	11,9
4 - 5	680	16,5
5 - 6	640	15,6
6 - 7	620	15,1
7 - 8	520	12,7
8 - 9	290	7,1
9 -10	110	2,7
10 -11	50	1,2

Tableau 2 : Distribution verticale des différentes catégories de graines sur 10 cèdres du peuplement du Mont Ventoux (Vaucluse)

Vertical distribution of different seeds on 10 cedars stand of Ventoux Mountain.

Hauteur en m (Nbre de cônes)	Total des graines (moyenne/cône)	Graines saines Nbre total (moyenne/cône)	Graines parasitées Nbre total (moyenne/cône)	Graines vides de taille normale Nbre total (moyenne/cône)	Graines vides de petite taille Nbre total (moyenne/cône)
0 - 1 (7)	859 (123±30)	485 (70±45)	13 (2±3)	105 (15±12)	256 (37±33)
1 - 2 (21)	2711 (130±12)	2193 (104±13)	93 (4±2)	213 (10±3)	212 (10±4)
2 - 3 (43)	5282 (123±8)	4276 (99±9)	146 (3±1)	458 (11±3)	402 (9±3)
3 - 4 (49)	6500 (133±6)	5159 (105±10)	222 (5±1)	683 (14±4)	436 (9±3)
4 - 5 (68)	8772 (130±8)	6869 (101±9)	329 (5±2)	1044 (15±3)	530 (8±2)
5 - 6 (64)	8390 (131±8)	6389 (100±8)	473 (7±2)	817 (13±3)	711 (11±3)
6 - 7 (62)	8273 (133±8)	5949 (96±9)	458 (7±2)	929 (15±4)	937 (15±3)
7 - 8 (52)	7266 (140±9)	5404 (104±10)	511 (10±3)	696 (13±3)	656 (13±3)
8 - 9 (29)	3890 (134±10)	2888 (100±10)	336 (11±4)	351 (12±4)	315 (11±4)
9 - 10 (11)	1446 (132±18)	1025 (93±22)	136 (12±5)	161 (15±5)	125 (11±4)
10 - 11 (5)	674 (135±7)	392 (78±48)	50 (10±10)	160 (32±62)	72 (14±7)

parasitées/cône augmente progressivement du bas vers le sommet des arbres. Les cônes de la cime sont donc davantage parasités. Le même résultat a été trouvé par SCHMID et al.,1984 pour Megastigmus albifrons WALKER sur Pinus ponderosa LAWS. Dans notre cas, le rapprochement de ces résultats avec la distribution verticale des cônes (tab.1) exclue une recherche au hasard de ces derniers par les femelles de M.suspectus. Les observations de terrain, ont par ailleurs montré que les femelles émergentes des graines situées sur le sol avaient effectivement tendance à s'envoler vers la cime des arbres.

31.3. Distribution des autres catégories de graines des cônes

Le nombre moyen de graines saines par cône varie de 70±45, entre 0 et 1 m, à 105±10, entre 3 et 4 m (tab. 2). Dans ce cas, l'analyse de la variance, après vérification de la normalité des données, donne une valeur de F = 1,10 (10 et 400 ddl) non significative, même avec α = 0,25, la variabilité entre les arbres étant trop importante. En effet, la même analyse, cette fois-ci entre les arbres donne F = 46,60 avec 9 et 401 ddl, le nombre moyen de graines saines/cône s'échelonne de 42, sur l'arbre 9, à 145, sur l'arbre 5. La comparaison multiple de ces valeurs, au seuil de 1 %, permet de distinguer 3 groupes d'arbres, dont les caractéristiques moyennes sont les suivantes :

1er groupe, 1 seul arbre, peu productif (300 cônes), dominé,

2ème groupe, 5 arbres, 362 cônes/arbre,
dominés, de 115 cm de circonférence et de 11 m
de hauteur,

3ème groupe, 4 arbres, le plus homogène, 500 cônes/arbre,
de tendance dominante, de 120 cm de circonférence
et de 12 m de hauteur.

Pour le deuxième et le troisième groupe, l'analyse de la variance du nombre de graines saines/cône donne, cette fois ci, des différences significatives entre les strates, les valeurs respectives de F étant de 2,26, avec 10 et 170 ddl et de 3,31, avec 10 et 189 ddl. Pour le deuxième groupe, le nombre moyen de graines saines/cône est faible entre 0 et 1 m et au-dessus de 9 m, la valeur minimum (64) étant entre 10 et 11 m. Pour le troisième groupe, constitué d'arbres dominants, les résultats sont comparables, mais c'est entre 10 et 11 m que l'on trouve le maximum de graines saines, 101/cône. Cette particularité, qui serait à vérifier dans le peuplement, est peut-être due à un supplément de lumière. Quoiqu'il en soit, ces analyses montrent qu'en règle générale, les strates de la partie médiane sont celles qui ont les valeurs les plus élevées. C'est là où le nombre de cônes et la biomasse végétale sont les plus importants.

Tableau 3 : Parasitisme comparé de Megastigmus suspectus à différentes hauteurs sur 10 cèdres du peuplement du Mont Ventoux (F = 5,00 ; ddl : inter pop. 10, intra pop. 400).

Comparative cones parasitism of Megastigmus suspectus on different levels of 10 cedars stand in Ventoux Montain (F = 5,00 ; dl between : 10 ; within : 400).

-Hauteur en m	Nombre de cônes	Nombre moyen de graines parasitée/cône Log (x+1)	Test de Duncan au seuil 1 %	5 %
9-10	11	2,39		
10-11	5	2,09		
8-9	29	2,07		
7-8	52	1,90		
6-7	62	1,58		
5-6	64	1,55		
3-4	49	1,28		
1-2	21	1,26		
4-5	68	1,20		
2-3	43	0,98		
0-1	7	0,57		

Le nombre moyen de graines vides de grande taille par cône varie de 10±3, entre 1 et 2 m, à 32±52, entre 10 et 11 m (tab. 2), cependant les analyses montrent que les différences entre les strates ne sont pas significatives (F = 1 pour 10 et 400 dl), ici encore la variabilité entre les arbres étant trop élevée. Dans ce dernier cas, F est égal à 46,6 pour 9 et 401 ddl. Les arbres peuvent être répartis en 2 groupes, mais aucun ne présente de différences significatives, du nombre de graines saines/cône, entre ses strates.

Le nombre moyen de graines vides de petite taille par cône varie de 8±2, entre 4 et 5 m, à 37±33, entre 0 et 1 m. Les différences entre les moyennes des strates sont ici nettement supérieures aux différences entre les cônes quelque soit la strate à laquelle elles appartiennent, F étant égal à 5,03, pour 10 et 400 ddl. La moyenne du nombre de graines vides de petite taille par cône de la première strate, au-dessus du sol, est différente des autres, au seuil de 5 %.

3.2. Comparaison des quadrants

La distribution des cônes sur les 10 arbres par secteur géographique est la suivante :

. Au nord, 390 cônes (9,5 %)
. Au sud, 1330 cônes (32,4 %)
. A l'est, 1200 cônes (29,2 %)
. A l'ouest, 1190 cônes (29 %).

Le nombre de cônes sur le quadrant nord est trois plus faible que celui des 3 autres quadrants. Dans ces derniers, la biomasse végétale est importante, au Nord, au contraire à cause des vents dominants (Mistral), les branches latérales ne sont pas développées.

La distribution par quadrant des différentes catégories de graines (tab 4) sont données pour les 10 cèdres. Les analyses (tab. 5) montrent que des différences existent entre les moyennes de chaque quadrant, du nombre de graines parasitées par cône. Pour ces dernières, sur les 10 arbres, les valeurs les plus importantes sont sur les secteurs nord et ouest, les plus faibles sur ceux du sud et de l'est. Là encore, l'origine doit, sans doute, être recherchée dans le comportement de ponte des femelles. Les arbres, les plus proches de ceux qui ont été échantillonés, sont pratiquement toujours situés au sud et à l'est, ce qui augmente leur effet silhouette, sur les secteurs nord et ouest. Dans le quadrant ouest, le nombre de graines saines par cône a tendance à être plus faible. La même différence existe aussi, pour le nombre total de graines par cône et celui du nombre total de graines de taille normale. Dans ces deux derniers cas les valeurs respectives de F sont de 2,38 (significative), et de 3,29 (très

Tableau 4 : Distribution par quadrant des différentes catégories de graines sur 10 cèdres du peuplement du Mont Ventoux.

Quaters distribution of different seeds on 10 cedars stand in Ventoux Montain.

Quadrant Orientation (Nbr.cônes)	Graines saines Nbr.Total % (moy/cônes)	Graines parasitées Nbr.Total % (moy/cônes)	Graines vides de taille Nbr.Total % (moy/cônes)	Graines vide de pte taille Nbr.Total % (moy/cônes)
Nord (39)	4094 105±8	309 8±3	502 13±4	346 9±2
Sud (133)	13726 103±5	807 6±1	1799 14±3	1414 11±2
Est (120)	12296 102±7	527 4±1	2016 17±3	1328 11±2
Ouest (119)	10916 92±6	1123 9±2	1299 11±1	1564 13±2

Tableau 5 : Comparaison des differentes catégories de graines, sur les 4 secteurs géographiques : analyse de la variance, valeurs de F significatives aux seuils de 5% (*), 0,5 % (***) ; comparaison multiple des moyennes (Duncan) au seuil de 10 %.

Comparison of different seeds on 4 geographical quarters : variance analysis, significative threshold of value : 5 % (*), 0.5 % (***) ; Duncan test with a threshold of 10 %.

	Graines saines (x)	Graines parasitées Log(x+1)	Graines vides de taille Log(x+1)	Graines vides de petite Log(X+1)
SOURCE DE VARIATION				
-entre les secteurs (carré moyen)	3744,56	10,2	1,59	1,23
-entre les cônes (carré moyen)	1178,68	1,16	0,70	0,65
-valeur de F (10 et 401 ddl)	3,18 *	8,63 ***	2,27	1,91
SECTEUR				
Nord (moy. cône)	105,0	1,7	2,3	2,1
Sud (moy. cône)	103,2	1,4	2,3	2,1
Est (moy. cône)	102,5	1,2	2,5	2,2
Ouest (moy. cône)	91,7	1,8	2,2	2,3

significative). Le fait d'avoir peu de graines saines sur les cônes de ce quadrant peut donc être considéré comme la double conséquence, d'une part d'un plus faible nombre de graines de taille normale, d'autre part du nombre plus élevé de graines parasitées. Enfin, aucune différence n'a pu être mise en évidence pour le nombre de graines vides quelque soit leur taille.

Les différences dans les quadrants seraient peut être liées à certaines caractéristiques propre au peuplement : exposition, vent dominant, isolement des arbres.

IV - CONCLUSION

Cette étude a montré que le nombre de graines parasitées par cône augmentait progressivement à partir du niveau du sol. Les attaques étaient plus élevées sur la cime des arbres. Des différences existent aussi entre les secteurs géographiques mais elles sont plus faibles et il faudrait s'assurer qu'elles ne dépendent pas de certaines caractéristiques propres au peuplement. Par ailleurs, ces résultats ont été établis sur 10 arbres fructifères, pourvus de branches basses, apparemment comparables. Malgré cela, des différences importantes apparaissent entre eux et il serait nécessaire de revoir cet aspect. Enfin, le taux d'attaques était relativement très faible et il serait nécessaire de reprendre cette étude pour des taux d'attaques plus élevés, bien que l'on se heurte souvent dans ce cas au problème de la rareté des cônes.

Quoiqu'il en soit, on tient compte des différences mises en évidence dans la récolte d'un échantillon destiné à la détermination du taux d'attaques d'un peuplement. Les cônes sont prélevés dans les différentes strates du houppier. Par ailleurs, pour la récolte des cônes destinés aux pépinières, on sait maintenant que ceux de la cime des arbres, difficile à atteindre, ne sont pas les plus intéressants. De même, sur les branches les plus basses, leur récolte est à éviter. Le nombre de graines saines a tendance à y être plus faible, celui des graines vides de petite taille plus important.

REFERENCES CITEES

BARBERO M., DU MERLE P., GUENDE G., QUEZEL P., 1978 - La végétation du Mont-Ventoux. In la terre et la vie, supplément, n°1, pp. 21-27.

BERLAND L., 1950 - Un chalcidien phytophage : Megastigmus suspectus Var. pinsapinis Hoff. Entomologiste, to. 6, n°2, pp. 56-57.

DAGNELIE P., 1975 - Théorie et méthodes statistiques. Applications agronomiques. Vol II. Gembloux : Presses agron. Gembloux.

FABRE J.P., 1986 - Dynamique des populations de Megastigmus suspectus Var. pinsapinis Hoff. (Hym. Torymidae) dans les cédraies du sud-est de la France. Proccedings of the cone and seed Insects Working Party Conférence, Working Party S2.07.01, I.U.F.R.O., Briançon, 3-5 septembre, pp. 127-145.

SCHMID J.M., MITCHELL J.C., CARLIN K.D., WAGNER M.R. 1984 - Insecte damage, cone dimensions, and seed production in crown levels of ponderosa pine. Great Basin Naturalist, vol 44, n°4, pp. 575-578.

TOTH J., 1978 - Contribution à l'étude de la fructification et de la régénération naturelle du cèdre de l'Atlas (Cedrus atlantica Manetti) dans le sud de la France. Thèse Docteur Ingénieur, Faculté des Sciences et Techniques de Marseille Saint-Jérôme, soutenue le 23 mars, 136 pp.

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CONTRIBUTIONS TO THE BIOLOGY OF THE JACK PINE TIP BEETLE, *CONOPHTHORUS BANKSIANAE* (COLEOPTERA: SCOLYTIDAE), IN MICHIGAN

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ABSTRACT

The jack pine tip beetle, *Conophthorus banksianae*, attacks the shoots of jack pine, *Pinus banksiana*, from mid-May until mid-September in Michigan. Early season shoot attacks are primarily for feeding, mid-season for reproduction, and end-of-summer attacks are for creating overwintering shelters. The mean rate of shoot attack/tree exhibits a dome-shaped curve over the course of the growing season. Numbers of shoots damaged per tree increases linearly with tree size. Jack pine tip beetles "handle" jack pine shoots in different manners than red pine cone beetles, *Conophthorus resinosae*, "handle" shoots of red pine, *Pinus resinosae*. The phenology of oviposition by the two beetles is also different.

INTRODUCTION

The jack pine tip beetle (JPTB), Conophthorus banksianae, is a shoot-infesting insect of pines, Pinus spp., in the Great Lakes Region. Although it has been recorded on four different host species, it is most prevalent on jack pine, Pinus banksiana. While the JPTB does not directly attack and kill jack pine cones, its chronic damage to jack pine shoots may indirectly reduce cone yields by lowering tree height growth and pistillate flower production. It, like other shoot-boring insects of pines, may keep trees in a stunted state of prolonged juvenility, producing primarily vegetative and staminate flower buds (Whitham and Moper 1985).

The jack pine tip beetle is morphologically identical to (though somewhat smaller) and sympatric with the red pine cone beetle (RPCB), C. resinosae, in parts of Michigan and Ontario. Although the JPTB has been described as a separate species (McPherson et al. 1970), its biology and behavior are still so poorly known that there is reason to suspect that it may merely be a behavioral variant of the RPCB, a species which exhibits plasticity in host species and host organ selection, depending on the relative availability of the preferred host species (red pine, Pinus resinosae), and the preferred host organs for reproduction (red pine cones) (Mattson et al. 1984, Mattson and Strauss 1986).

For example, it is known that both species sequentially exhibit three biologically different stages of shoot attacking behavior: (1) overwintering/feeding attacks, (2) feeding/breeding attacks, and (3) reproductive attacks. Overwintering attacks occur at the end of the growing season in the tips of new shoots for the purpose of creating an overwintering shelter (hollowed buds), and for acquiring energy and nutrients to sustain individuals through the dormant season. Feeding attacks are primarily for nutrition after emergence from overwintering, but mating may also occur. Reproductive attacks are for the purpose of mating and oviposition.

The goal of this study was to learn more about the seasonal phenology and shoot-attacking (for feeding and reproduction) behavior of JPTB to allow comparisons with the phenology and cone- and shoot-attacking behavior of RPCB. This study also tested the hypothesis that the number of attacked shoots per tree is a function of tree size, a pattern which has been found for RPCB on red pine (Mattson and Strauss 1986).

METHODS

This study took place in 1985 and 1987-1988 in an open grown, 14-16 year-old jack pine forest on sandy soils in southern Kalkaska County, Michigan (T25N, R6W, Sec. 24). Tree height and

stem density averaged 3.2 m and 543/ha in 1987 respectively. This area has been chronically infested with JPTB since at least 1983 when I first observed a large number of JPTB-killed shoots. On 20 May 1987, I randomly selected 25 trees within a 1-ha plot for monitoring the number of beetle-attacked shoots per tree. Eight more trees were added on 5 June 1987. Thereafter, I reexamined these trees on a 2-4 week schedule, giving a total of five or six measurements per tree by the summer's end. On each date we counted and marked with plastic flagging the number of attacked shoots since the last examination. Two observers, each on opposite sides of the tree, walked slowly in two complete circles about the tree counting and marking shoots. On tall trees, we used a 3-meter tripod ladder to examine the upper crown. Newly attacked shoots are distinguished by either or both of two traits: (a) presence of a small resinous pitch tube on the side of the shoot, and (b) a slight wilting and reddening of the needles near the apex of the shoot. Attacks occurring in brown, woody shoots formed the previous year were flagged with a different color to distinguish them from attacks in current-year green shoots.

In August 1987, I collected 25 newly attacked shoots to monitor oviposition and to measure galley construction. In August 1988, I randomly collected 160 JPTB shoots to compare characteristics of their attacks with those of RPCB on red pine shoots (n = 139) in a natural red pine stand near St. Ignace, Michigan, at the same time. In the laboratory, I measured total length (shoot base to bud tip) of the newly attacked shoots and the distance of the Conophthorus entrance from both the base of the shoot and from the base of the bud. These latter two variables were plotted against one another to compare the actual positions of C. banksianae and C. resinosae entrance holes on new shoots. Because shoot lengths were so highly variable, I also calculated the relative height of all entrance holes by dividing their distance form the shoot base by the total length of the shoot below the bud. These data were analyzed by creating a frequency distribution showing the percentage of shoots with entrance holes in different relative height classes, using class increments of tenths (0-10, 11-20, etc.).

In October 1987, I measured the heights and basal diameters (ground line) of all trees, and classified all flagged shoots according to their position in one of three vertical crown strata (lower, middle, and upper zones).

RESULTS AND DISCUSSION

Phenology of Shoot Attack

On the very first sample date, 20 May 1987 (Julian day 140), there were already 5.56 (SD = 9.67, n = 25) shoots attacked per tree. During the next 16 days, attacks/tree accrued at the rate

of 0.18/day or 1/5.5 day. Between 5 June (Julian day 156) and 17 June (Julian day 168), attacks accrued at the rate of 0.47/tree/day (Figure 1). Therefore, during the first 28 days since 20 May, shoot attacks increased on the average only 0.30/tree/day, or approximately one new shoot per tree every 3.3 days. Thereafter the rate of attacks increased markedly (Figure 1). For example, during the 27-day period following 17 June, the average rate was 1.13 new shoots attacked/tree/day, or about four-fold the previous month's rate. This rate was sustained for still another 3 weeks, until 1 August (Julian day 213), during which time it averaged 1.21/tree/day. Subsequently, it declined precipitously because during the next 46 days, trees accrued on the average only six more attacks, or less than one every 7-8 days. At the end of the summer (16 September) trees averaged 96.2 (SD = 69.7, n = 33) damaged shoots per tree (not counting recent overwintering attacks, mean = 4.3/tree), although the range was 14 to 292.

The dramatic increase in the daily rate of shoot attacks per tree during mid-late June had been casually observed in two previous years (1984, 1985) and by McPherson (1968). This sudden rise in activity was also linked to a change in the location of JPTB shoot entry. For example, up until mid-June, all attacks were confined to the old wood, just immediately below the bud or the base of the newly elongating shoot. After mid-June, all attacks were confined to the tip of the new shoot growth, just a few millimeters ($\bar{x}$ = 5.9 mm, SD = 3.4, n = 29 in 1987, $\bar{x}$ = 6.4 mm, SD = 3.8, n = 37 in 1985) below the base of the bud. Almost all attacks occurred within 25 mm of the bud, but on rare occasions, probably less than 1 in 100, attacks occurred lower on the new shoots but always much above their midpoint (see later discussion). This change in both the rate and location of shoot attacks was tied to the completion of shoot elongation (Hall 1972) (Figure 2). For example, on 17 June 1987 shoot elongation was 98% of its maximum for that year when the beetles suddenly changed into a new behavioral mode for shoot attack. McPherson (1968) hypothesized that the early attacks in old wood are strictly for feeding whereas later ones were for oviposition. Hall (1972) made the same conclusions. This implies that beetles apparently feed in the shoots for about 30-45 days before beginning reproduction in the fully elongated, new shoots. Herdy and Thomas (1961), however, found that oviposition occurred much earlier (24 May) in Ontario. I cannot substantiate whether beetles reproduced in their early season attacks in 1987, but they did in 1985 because I recovered second-instar JPTB larvae from such attacks on 20 and 26 June. Hence, I conclude that oviposition does occur in some of the early season attacks on old wood, but most takes place in the new shoots following cessation of shoot elongation. In fact, the length of JPTB oviposition galleries in these shoots was a linear function of the distance between the entrance hole and the tip of the bud on that shoot (Figure 3). From the entrance holes, beetles always bored distally into the bud, just as McPherson (1968) reported.

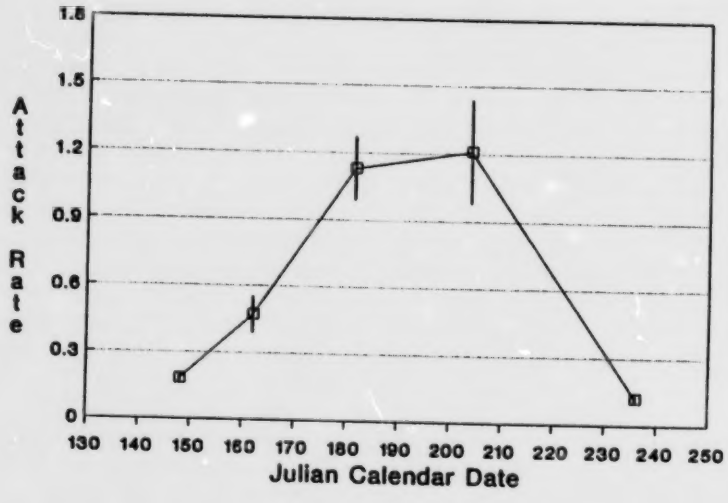

Fig. 1. Comparing differences in the rate of shoot attack (mean no./day/tree ± 1 SD) by C. banksianae on jack pine in 1987. Each mean is plotted against the midpoint of its respective time period.

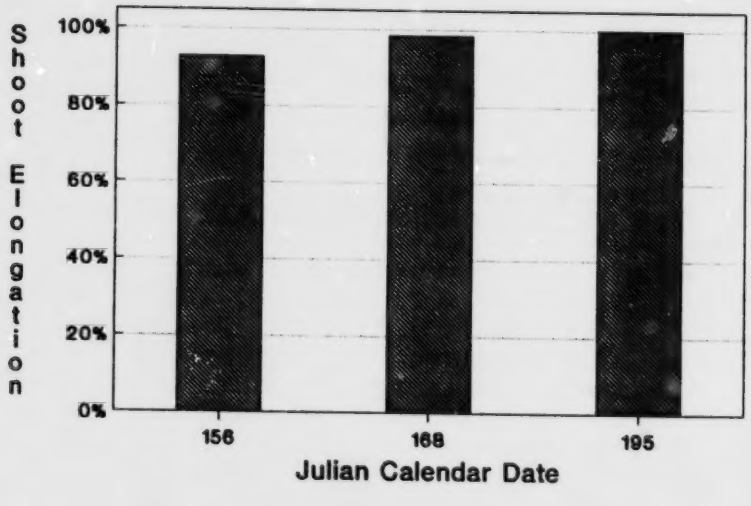

Fig. 2. Percentage of maximum annual shoot elongation by jack pine on different dates in Kalkaska Co., Michigan, 1987 (n = 25 trees).

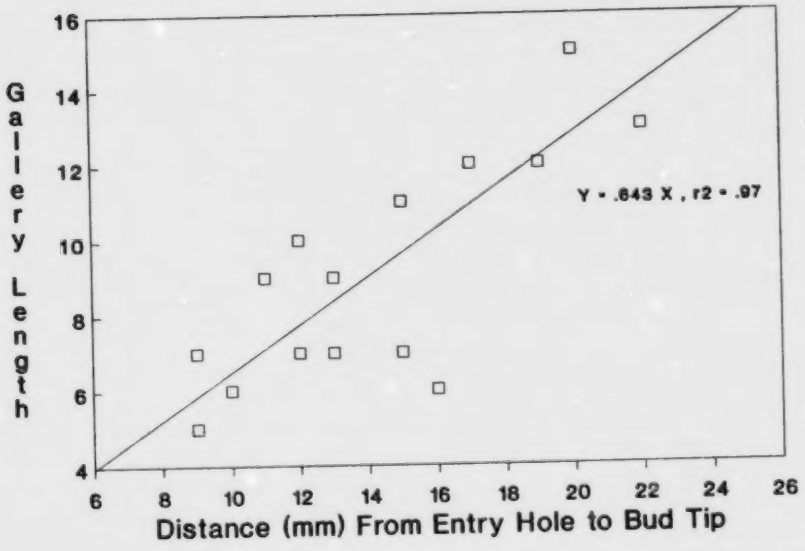

Fig. 3. Total length (mm) of oviposition galleries by C. banksianae in jack pine shoots in relation to available room for gallery construction.

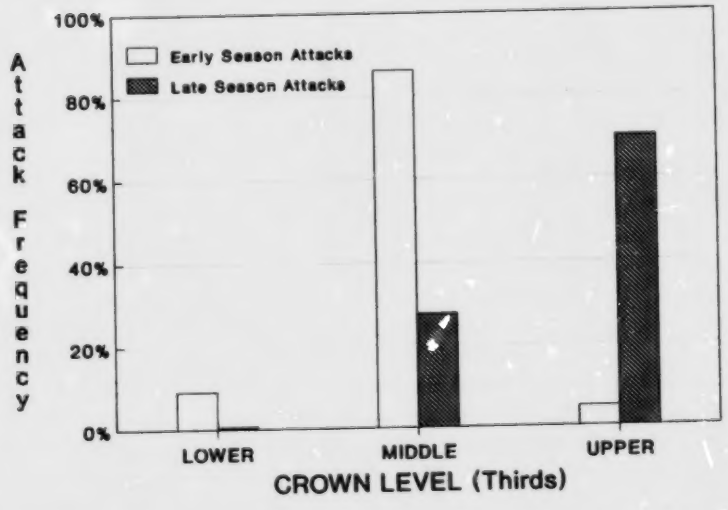

Fig. 4. The frequency distribution (%) of early (2 May-17 June) and late-season (July-August) attacks among the upper, middle, and lower crown thirds of jack pine.

Position of Attacked Shoots

There was a trend for the early season attacks to occur much lower in the crown than the late season attacks. Moreover, they were often on weak lateral branchlets rather than on more vigorous terminal branchlets. Classifying attacks according to their distribution among crown zones substantiated this impression (Figure 4). The center of distribution for early-season feeding/reproductive attacks was in the midcrown with the remainder divided between lower and upper crowns in a ratio of 2:1. On the other hand, late-season reproductive attacks were clearly centered in the upper crown, just as Hall and Wilson (1974) found, with the balance largely occurring in midcrown.

The occurrence of early-season attacks in the lower two-thirds of the trees spawned the hypothesis that the newly emerging spring beetles crawl from the litter where they overwinter up into the tree canopies, instead of flying into them as do other species of Conophthorus. I tested this hypothesis in 1988 by selecting 20 pairs of trees on 20 April, half of which I banded with a 30 cm wide strip of Tanglefoot near the ground to prevent insects from crawling into the trees. On 17 May, I counted the number of JPTB attacks occurring on all trees ($\bar{x}$ = 8.7/tree). The mean difference among the 20 paired trees was not significantly different from zero ($\bar{x}$ diff = -0.10, SD = 3.7). Therefore, the crawling hypothesis has to be rejected in favor of the flying hypothesis. Although I could not detect any beetles in the trees on 20 April when the Tanglefoot bands were applied, there is a very remote chance that the beetles had already occupied the trees.

Attacks Per Tree In Relation To Tree Size

On any given date there was substantial variation in the number of attacked shoots per tree as witnessed by the large standard deviations associated with the mean tree counts (see "Phenology of Shoot Attacks"). One hypothesis to explain such differences among trees is the target-area hypothesis. This hypothesis supposes that beetles move like random projectiles, and the number of them or their attacks per tree will be a linear function of the total target area per tree for stopping such "missiles." Target area might be directly related to crown surface area, numbers of shoots, numbers of cones, or some other variable associated with size.

One of the principle objectives of this analysis is not only to explain tree-to-tree variation but to uncover information about the underlying mechanisms by which beetles find/accept hosts (Mattson et al. 1984, Mattson and Strauss 1986). For example, if beetles colonize and occupy trees on the basis of some special cues emanating from the tree organs that they

utilize for reproduction, one might expect numbers of beetle attacks to increase in a non-linear fashion (e.g., sigmoidally, exponentially, logarithmically, etc.). Typically one would expect some sort of threshold phenomenon, as might be exemplified by exponential or sigmoidal beetle response curve to the amount of cue available per tree. At low levels of the cue, few beetles would colonize the host tree, whereas after surpassing some threshold amount of cue, colonization would substantially rise. On the other hand, if beetle response always conforms linearly to the amount of cue or amount of resource, the implication is that the host-finding process can be most simply explained by random movement of beetles that are highly prone to arrestment once having accidentally entered a plume of any amount of cue.

Data for RPCB attacks on red pine cones always conform to the linear model. In other words, branches and trees with very few cones have the same proportion of their cones attacked as branches and trees with many cones (Mattson et al. 1984, Mattson and Strauss 1986). Obviously, when one uses attacked cones as an index of beetle response, it can never exceed the total amount of available cones, and therefore when beetle populations are extremely large relative to cones, one would expect the response relationship to be necessarily linear with cone abundance. However, as Mattson et al. (1984) demonstrated, the beetle response relationship is linear under all conditions of beetle and cone abundance. Likewise, number of RPCB shoots per tree showed a linear increase with the tree's crown surface area (Mattson and Strauss 1986).

Because jack pine crown shapes were so highly variable and therefore crown surface areas difficult to estimate, I regressed JPTB shoots attacked per tree against tree basal area (π x $diam^2/4$) at ground line. Crown size is known to be closely linked to tree basal area (Brown 1978, Stanek and State 1978). For each of six sampling dates, number of JPTB shoots per tree was a linear function of tree basal area, the intercept not differing from zero except at one time (14 July) (Figure 5). The variance about the regressions, however, increased with time and with tree basal area. The change in beetle shoot-attacking behavior in late June was clearly evident from the substantial increase in the slope of the regressions between Julian dates $\geq$ 195 and those $\leq$ 168. Hence much of the tree-to-tree variation in shoot damage can be explained by tree size. Moreover, it also appears that trees are attacked largely in proportion to how much target area they offer to "searching" beetles.

Cumulative Shoot Damage Per Beetle

If one assumes that the beetles occurring in shoots in May represent the entire population that creates all of the subsequent shoot injury, one can then estimate the number of shoots attacked per season per individual beetle. For example, each damaged shoot in May usually has on the average one beetle

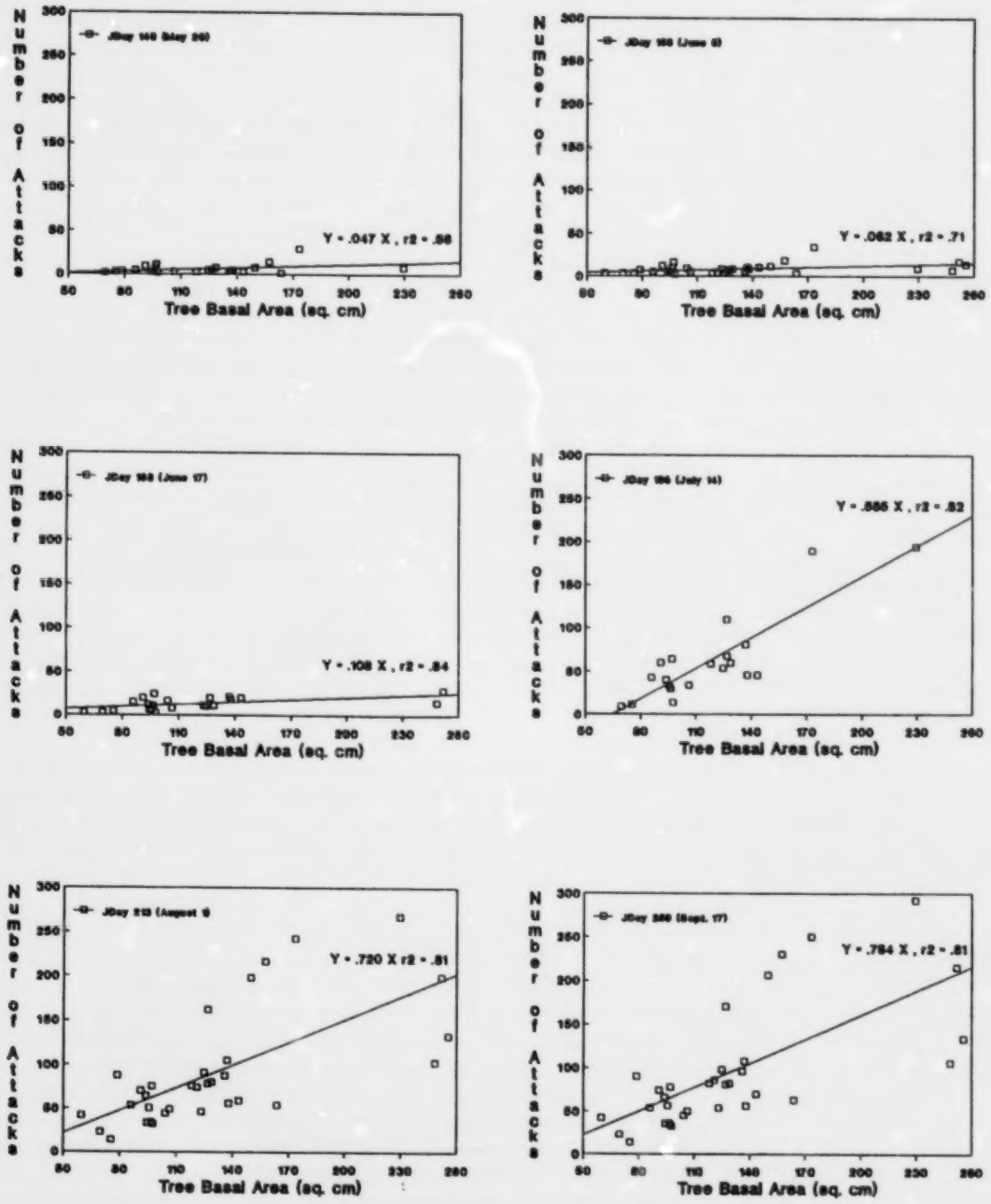

Fig. 5. Number of shoots per jack pine tree attacked by C. banksianae on different dates in 1987 plotted against tree basal area at ground line.

(59 beetles found in 62 shoots on 5/15/85). Using late May as our beetle population index date, there were about six beetles/tree in 1987. In September there were an average of 96 damaged shoots/tree. This implies that each beetle attacked an average of 16 shoots during the course of the summer, assuming that both males and females attacked shoots. If, however, the sex ratio is close to 1:1 and only females attack shoots after the early feeding attacks by both sexes in May, then the starting female population in May was about three beetles per tree and the total number of reproductive attacks was about 90/tree. This translates to about 30 shoot attacks/female. Because the majority of attacks occur between mid-June and mid-August, a period of 60 days, three females per tree must move to a new shoot every second day to finish 30. This seems entirely feasible if they construct galleries at the same rate as the red pine cone beetle (2.3 hrs/mm @24°C) because JPTB galleries in this area averaged only 10 mm long. However, we know that some early-season attacks in May and June probably produce adult progeny by early July. If they attack the newly elongated shoots as do their parents, then it is not possible to estimate the number of shoots killed per female by the preceding methods.

Comparing Behavior of Jack Pine Tip Beetle and Red Pine Cone Beetles

The seasonal pattern of shoot-boring behavior of JPTB and RPCB's seem markedly different. For example, JPTB attacks shoots and rarely cones of jack pine from early May until early August. On the other hand, RPCB preferentially attacks red pine cones if available from early May to early July. However, if at any time cones become scarce or cones begin to harden off, RPCB's attack shoots (Lyons 1956, Mattson 1980). Consequently in early to mid-July, shoot attacks may dominate over cone attacks. At this time RPCB behavior exactly parallels that of JPTB. The propensity of RPCB to attack jack pine cones is low but not negligible as apparently is the case for JPTB (McPherson *et al*. 1970, Herdy and Thomas 1961).

The phenology of reproduction by the JPTB in Michigan is displaced about 2-3 weeks after that of the RPCB. For example, peak oviposition by RPCB occurs from early June to mid-July (Mattson 1980). On the other hand, peak oviposition for JPTB occurs from late June to early August (McPherson *et al*. 1970a, Hall and Wilson 1974a). RPCB's compete intensely with one another and other cone insects for cones (Mattson 1986), so there may be strong selection pressure for early cone attack and oviposition. On the other hand, it seems that there is selection pressure from the host plant to delay significant JPTB oviposition until new shoots have completed their elongation. I can offer no explanation for the JPTB's apparent need to wait until shoot elongation has ceased.

One tenable hypothesis is that elongating pine shoots, especially those with narrow diameters, like jack pine on poor soils, are extremely fragile when injured and consequently fall to the ground and desiccate (Dr. P. Niemela, personal communication). Diameters of jack pine shoots at the point of attack average about 4.4 mm (SD = 0.59, n = 20) (Hall and Wilson 1974a) whereas those of red pine shoots average 7.4 mm (SD = 1.4, n = 15), almost twice as much. Adult female JPTB average 1.1 mm in width and about 2.8 mm in length (McPherson 1968). A second is that buds are the only important food resource on narrow diameter jack pine shoots, and hence beetles must wait for shoot elongation and, more importantly, bud development to conclude. JPTB galleries extend into the buds and larvae and pupae are usually found there. A third hypothesis is that host plant defenses may prevent beetles from attacking the new shoots until they are fully elongated. Although there is no strong direct evidence to support this speculation, indirect evidence suggests that vigor of shoots may be important to JPTB. For example, in early spring, the first shoot attacks occur on the smallest diameter, least vigorous lateral branchlets in the lower half of the tree crowns. These branch units may be less able to pitch-out or otherwise deter beetles than more vigorous units. Later, as buds break and shoot elongation starts, JPTB attacks larger more vigorous branchlets, but always in old wood below the point of new shoot extension. Another line of indirect evidence is the very spotty and limited geographic distribution of JPTB which contrasts with that of its host, jack pine. Is JPTB only capable of attacking stressed populations of trees as McPherson (1968) stated was the case for JPTB populations on red pine? Herdy and Thomas (1961) reported that JPTB was most common in Ontario on small trees growing in the open, just as typically occurs in Michigan.

The manner in which JPTB and RPCB "handle" new shoots is entirely different. In northern lower Michigan, JPTB attack new shoots only after they complete elongation, whereas RPCB attack new shoots in all stages of development. JPTB enter shoots about 6 mm below the base of the bud (Figures 6, 7). Not so for RPCB, which enter new shoots anywhere along their length except for the very top next to the bud (Figures 6, 7). There is a tendency, however, for RPCB to attack new shoots near their base early in the growing season and nearer the top later in the growing season. Therefore, depending on when RPCB begin shoot attacks, the relative positions of their entrance holes may vary. The samples used for Figures 6 and 7 contained RPCB shoots which were attacked during the entire growing season. JPTB extend their galleries into the developing bud, but this is not the case for RPCB. In 1987, about 40% of the average JPTB gallery length was contained in buds. Although these data tell us how each species typically performs on its customary host, they unfortunately do not tell us how each would perform when switched to the other's host plant. The data suggest, however, that the JPTB in Michigan is behaviorally different from RPCB and therefore would maintain

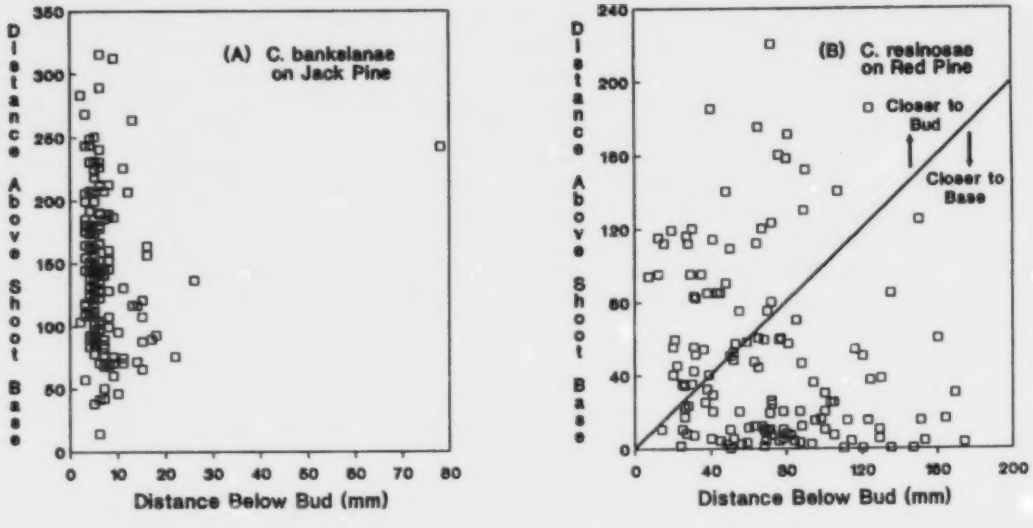
(A) C. banksianae on Jack Pine
Distance Above Shoot Base
Distance Below Bud (mm)
(B) C. resinosae on Red Pine
Closer to Bud
Closer to Base
Distance Above Shoot Base
Distance Below Bud (mm)

Fig. 6. Comparing the positions of gallery entrance holes by C. banksianae and C. resinosae by plotting the distance (mm) of each from the base of the shoot (Y axis) against its distance from base of bud (X axis). Holes equidistant from shoot base and bud would fall on the 1:1 line as in B.

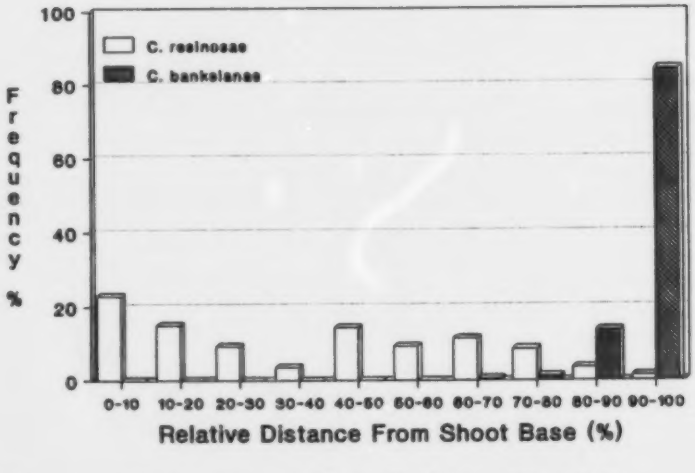

Fig. 7. The frequency distribution (%) of C. resinosae (n = 160) shoots having entrance holes at different relative distances from the shoot base. Relative distance = height of entrance hole ÷ total shoot length below bud x 100.

its unique shoot-handling behavior on other pine species as was implied by McPherson (1968).

Finally, there is the question about the flight behavior of JPTB relative to that of RPCB. The latter flies 10 to 25 m upward from their overwintering sites on the forest floor into the canopy of cone-producing red pines for spring feeding attacks. The JPTB, on the other hand, flies into small, open-grown trees, the tops of which are usually less than 5 m from the forest floor (McPherson 1968, Hall and Wilson 1974, Herdy and Thomas 1961). In late June to early July, RPCB apparently fly to small, understory red pine where they begin attacking shoots in addition to their usual attacks on shoots and cones in the tall overstory trees (Mattson and Strauss 1986). At this time, then, RPCB flight and host "searching" behavior nearly parallels that of JPTB. All of the information about JPTB and RPCB suggests that they are similar in many ways and closely related. Moreover, it seems that the JPTB is derived from the latter because its behavior is a canalized subset of the latter's.

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LITERATURE CITED

Brown, J. K. 1978. Weight and density of crowns of Rocky Mountain conifers. USDA Forest Service Res. Paper INT-197. 56 p.

Hall, D. J. 1972. The within-generation mortality, within-tree distribution, and damage of the jack pine tip beetle, Conophthorus banksianae McPherson. Ph.D. Dissertation, Michigan State University. University Microfilms, Ann Arbor, MI.

Hall, D. J. and L. F. Wilson. 1974a. Within-tree distribution of the jack pine tip beetle, Conophthorus banksianae McPherson, on jack pine. Great Lakes Ent. 7: 89-93.

Hall, D. J. and L. F. Wilson. 1974b. Within-generation mortality of the jack pine tip beetle, Conophthorus banksianae McPherson, in Michigan. Great Lakes Ent. 7: 151-162.

Herdy, H. and J. B. Thomas. 1961. The seasonal development of a species of Conophthorus (Hopkins) (Coleoptera: Scolytidae) in the shoots or jack pine, Pinus banksiana (Lamb.), in Ontario. Can. Ent. 43: 936-940.

Lyons, L. A. 1956. Insects affecting seed production in red pine I. Conophthorus resinosae Hopk. (Coleoptera: Scolytidae). Can. Ent. 88: 599-608.

McPherson, J. E. 1968. Non-morphological separation of a Conophthorus population found on jack pine from Conophthorus resinosae Hopkins, with description of a new species, Conophthorus banksianae (Coleoptera: Scolytidae). Ph.D. Dissertation, Michigan State University, University Microfilms, Ann Arbor, MI.

McPherson, J. E., L. F. Wilson, and F. W. Stehr. 1970a. A comparison between Conophthorus shoot-infesting beetles and Conophthorus resinosae (Coleoptera: Scolytidae) I. Comparative life history studies in Michigan. Can. Ent. 102: 1008-1015.

McPherson, J. E., F. W. Stehr, and L. F. Wilson. 1970b. A comparison between Conophthorus shoot-infesting beetles and Conophthorus resinosae (Coleoptera: Scolytidae) II. Reciprocal host and resin toxicity tests; with description of a new species. Can. Ent. 102: 1016-1022.

Mattson, W. J. 1980. Cone resources and the ecology of the red pine cone beetle, Conophthorus resinosae (Coleoptera: Scolytidae). Ann. Ent. Soc. Amer. 73: 390-396.

Mattson, W. J. 1986. Competition for food between two principal cone insects of red pine, Pinus resinosa. Environ. Ent. 15: 88-92.

Mattson, W. J. and S. H. Strauss. 1986. Are host volatiles involved in cone finding by Conophthorus resinosae? pp. 185-204. In A. Roques (ed) Proceedings of the 2nd Conference on Cone and Seed Insects. Station de Zoologie Forestiere. INRA-CRF Ardon, 45160 Olivet FRANCE. 312 p.

Mattson, W. J., B. E. Tabashnik, and J. R. Miller. 1984. Developing a conceptual model of cone finding behavior by the red pine cone beetle, Conophthorus resinosae Hopkins (Coleoptera: Scolytidae). pp. 65-76. In H. O. Yates (ed) Proceedings of the Cone and Seed Insect Working Party Conference. S. E. For. Exp. Sta. Forestry Sciences Lab., Carlton St. Athens, GA. 214 p.

Stanek, W. and D. State. 1978. Equations predicting primary productivity (biomass) of trees, shrubs, and lesser vegetation based on current literature. Canadian Forestry Service, Pacific Forest Res. Centre. Victoria, B.C. 58 p.

Whitham, T. G. and S. Moper. 1985. Chronic herbivory: Impacts on architecture and sex expression of pinyon pine. Science 228: 1089-1091.

HOST RELATIONSHIPS IN THE DOUGLAS-FIR TWIG MINING BEETLE, PITYOPHTHORUS ORARIUS BRIGHT (COLEOPTERA: SCOLYTIDAE), IN A NORTHERN CALIFORNIA SEED ORCHARD

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Abstract
The geographic range of the Douglas-fir twig beetle, Pityophthorus orarius Bright, has been extended beyond the original provenance of southern British Columbia to northern California. A survey of 457 Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) trees in 1985 revealed that those bearing especially heavy cone crops were significantly more likely to be infested by the twig beetles than were those bearing a light crop. Furthermore, a highly significant association was found between clonal source and attack rate.

Key words: Douglas-fir, seed orchards, Pityophthorus orarius

Résume
Le répartition géographique du scolyte des brindilles du sapin de Douglas (Pseudotsuga menziesii [Mirb.] Franco), Pityophthorus orarius Bright, était étendu au dela de l'ancien provenance du sud de la Colombie britannique au nord de la Californie. Une enquête de 457 sapins de Douglas en 1985 révélait que ceux portants des grandes récoltes des cônes étaient plus sensible à l'attaque que ceux avec des récoltes inférieurs. En outre, on a trouvé une association significative entre clone et taux d'attaque.

Mots-clefs: sapin de Douglas, vergiers à graines, Pityophthorus orarius.

INTRODUCTION

Research in conifer seed orchards tends to focus on pest species that destroy cones and seeds during the final growing season, because cone crops are most visible then and damage is more noticeable. In Douglas-fir, however, vegetative and conebud primordia are laid down a full year before the conebuds open for pollination, and eighteen months before cone maturation (Allen and Owens 1972). Insects that damage cone buds at this early stage are often overlooked as cone and seed pests, especially if the insects are cryptic in habit.

One such insect is the Douglas-fir twig beetle, Pityophthorus orarius Bright, a scolytid which mines the pith of Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) twigs. It has previously been reported only from southern regions of British Columbia, Canada (Bright 1968; Hedlin and Ruth 1970). Although Hedlin and Ruth (1970) and Bright (1981) predicted that its range would eventually be found to coincide more completely with that of its host, there have been no subsequent reports of it outside of British Columbia. The presence of the twig beetle is easy to overlook, however, because its most visible symptom is flagged twigs, which are fragile and often fall to the litter shortly after adult emergence in the late summer. For most of the year, the presence of these beetles goes largely undetected.

Most of the species in the genus Pityophthorus are regarded as nonpests or even as beneficial insects since most infest suppressed limbs, twigs, and branches of injured or felled trees, thus enhancing natural pruning and decomposition of slash (Chamberlin 1958; Bright 1981). P. orarius, unlike most species in the genus, mines and kills the tips of apparently healthy twigs. These terminals bear two generations of cones: the primordia of the ovulate strobili for the subsequent season's cone crop and the currently developing conelets. Each beetle attacks and mines two twigs during the completion of its life-cycle: one in which larval development is completed and one in which young adults overwinter (Hedlin and Ruth 1970). Hedlin and Ruth (1970) reported rates of attack of 1 to 2 twigs per square foot of foliage, with more than 100 attacks per tree in some cases. Depending on the size of the cone crop, then, a sizable number of both first-year and second-year cones could be destroyed by these beetles.

Here we report results of a survey in a coastal northern California Douglas-fir seed orchard which was undertaken in order to determine extent of twig beetle infestations, distribution patterns, and factors that might explain those patterns.

METHODS

In the summer of 1985, we discovered an infestation of P. orarius in the Louisiana-Pacific Corporation's Little River Seed Orchard, located about 10 km inland from Trinidad Head in Humboldt County, California (elevation 91 m). This seed orchard, which is located in a valley in the middle of the redwood/Douglas-fir timber type, originally consisted of 3,000 grafted clonal

Douglas-fir trees (100 clones X 30 ramets/clone) on about 6 hectares. Most of the grafts were performed in 1968.

Flagged twigs were first noticed in early August of 1985. Dissections of these flagged twiglets revealed larvae, pupae, and both teneral and fully-tanned adults in the mined twigs. Beetle galleries and external appearance of twigs were indistinguishable from those attributed to P. orarius by Ruth (1980). The species identity was later confirmed by D. E. Bright, Jr., who described the species (Bright 1968). Voucher specimens are on file at the Biosystematics Research Institute, Ontario, Ottawa, Canada.

In view of the potential impact of this insect in a seed orchard where resources are concentrated, we surveyed infestation rates on all trees within eight adjacent 100-tree plots in 1985. Owing to graft-union failure, only 457 trees remained in these eight plots. These trees represented 39 different clonal sources, with numbers of ramets per clone ranging from 4 to 19. We assessed infestation levels by tallying numbers of flagged twigs per tree. Flagging that is visible in the late summer is the result of brood galleries; damage caused by overwintering adults becomes apparent later in the year. Because a number of twig pathogens cause similar flagging, we used the following procedure to verify the cause of damage: ten trees were randomly chosen at each of two infestation levels (1-5 flagged twigs/tree and 6-10 flagged twigs/tree); then all flagged twigs were dissected from these twenty trees and causal agents were determined.

A separate survey had been performed during the previous fall in order to locate trees with especially large numbers of cone primordia. In this survey, reproductive buds were identified visually using the method of Allen and Owens (1972) and trees were ranked into either a "high" or a "low" cone-crop category. This procedure permitted us to evaluate the effect of cone crop on rate of attack by twig beetles.

Two-way analysis of variance (Anonymous 1982) was performed on numbers of beetles per tree (as measured by flagged twigs) using clonal source and predicted cone crop as main effects in the model. Because we anticipated an interaction between predicted cone crop and clonal source (ramets from the same parent are thought to flower in synchrony), we performed the analysis both with and without the interaction term in the model so that we could determine its impact on the root mean squared error (an indicator of the predictive value of the model).

Results and Discussion

The range of P. orarius is, as suspected, much greater than previously reported. It is not yet known whether the insect's distribution from southern British Columbia to northern California is continuous, but it seems likely given the unbroken distribution of the host type between those two locations. Careful observation of orchards in the late summertime may reveal its presence throughout the Pacific northwestern United States.

Dissections showed that, of the twigs which were randomly sampled for dissection, only 4.6% (5 out of 108) were killed by agents other than twig beetles. In this instance, then, flagged twigs were a highly reliable indicator of beetle infestation levels. Our survey revealed that in August of 1985, 56.0% of the seed orchard trees were infested with P. orarius. The average infestation rate was 4.4 twigs/tree (range = 1 - 79 twigs/tree). Although this number seems quite low, it is a conservative estimate since

some infested twigs may already have fallen off and some may not yet have changed color.

Three-dimensional plots of attack rates per tree for 1985 (Fig. 1) show an apparent tendency for aggregation by the beetles. This apparently contagious distribution could be caused by factors such as oviposition, aggregation pheromones, host kairomones, microclimate, or clonal susceptibility. Although the orchard was designed to maximize the distance between ramets from the same clonal source, the ramets were planted in repetitive sequences such that the clonal source of a ramet's immediate neighbors was constant throughout the orchard. Thus, if clonal susceptibility exists and susceptible clones happened to be adjacent, a contagious distribution could result as an artifact of the orchard design.

The analysis of variance revealed a highly significant interaction between predicted crop and clonal source ($P=0.0008$). In general, a highly significant interaction term prevents further analysis of main effects in analysis of variance. However, removing the interaction term from our model increased the root mean squared error by an insignificant amount, so we proceeded with evaluation of the results without the interaction term. This analysis revealed a highly significant association of beetle attack rate with both clonal source and predicted cone crop ($P=0.0002$ for the model with conecrop and clone as main effects). Trees with heavy conecrops had significantly more beetle attacks per tree than those bearing light crops (7.3 compared to 3.7).

Mean attack rates per tree by clone, with 95% confidence limits, are shown in Fig. 2. The mean rates of infestation ranged from 0.13 beetles/tree for clone 499 to almost 13 beetles/tree for clone 443, nearly a 100-fold difference. Given the large number of clones, the low average attack rate, and the interaction with crop level, we decided that pairwise testing for differences between clones would be pointless. It is interesting to note, however, that a few clones (438, 443, 461 and marginally 435) had exceptionally high rates of attack.

Only two highly susceptible clones were adjacent to one another (435 and 438); thus the clustering of susceptible clones was too infrequent to explain the contagious distribution of the beetles. Because the seed orchard appears remarkably homogeneous over the scale of the beetle aggregations, it does not seem likely that microclimate could explain such a distribution either. We furthermore noted that beetle distributions appeared to be clumped within trees, with many attacks on a single or a few branches per tree. It seems most likely, then, that this aggregation phenomenon is a function of either oviposition or semiochemicals.

Mattson (1980) defines two classes of herbivores: those that are morphologically adapted for exploiting nutrient-poor mature plant biomass, and those with behavioral adaptations for exploitation of rapidly-growing plant tissues, such as fruits, seeds, and developing shoots, that have higher nutrients levels and lower levels of fiber and toxic compounds. Kramer and Kozlowski (1979) report that, in Douglas-fir, carbohydrate reserves are translocated from one-year-old shoots to expanding new shoots from April to early June, coinciding with the attack period of adult twig beetles (Hedlin and Ruth 1970). However, fruits and seeds are powerful competitors for nutrients, and food is transported to them at the expense of vegetative growth (Kramer and Kozlowski 1979). Reproduction utilizes a large proportion of total woody plant carbohydrate and nitrogen reserves (Kramer and Kozlowski 1979); thus the selective attack of more fecund trees by twig beetles may be a behavioral adapation of the sort described by Mattson (1980) to intercept

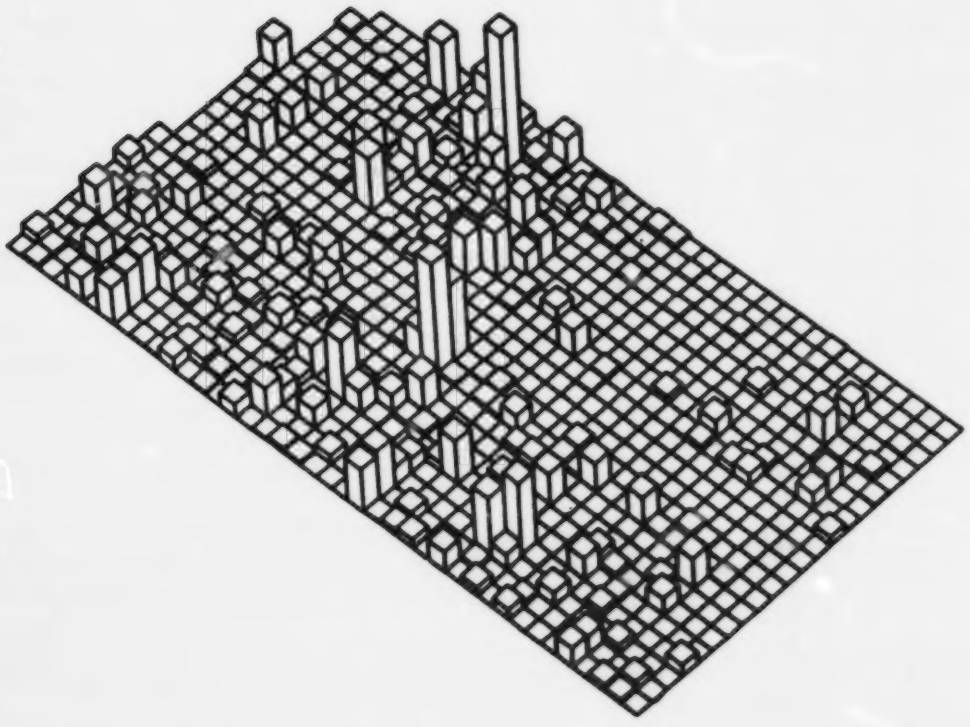

Figure 1:Three dimensional plot of attack rates per tree by Pityophthorus orarius, Little River Seed Orchard, 1985. Vertical bars represent individual trees, with bar height proportional to attack rate). Seed Orchard, August, 1985.

CLONE NUMBER	N	MEAN ATTACKS PER TREE	STDEV
405	11	3.364	6.830
429	11	3.455	4.824
430	12	1.833	2.887
431	8	3.500	3.024
432	11	7.273	11.808
433	11	1.818	3.371
434	6	1.333	2.338
435	14	10.357	10.938
438	6	11.000	13.565
439	13	3.385	5.189
440	13	5.231	7.897
441	9	0.444	1.014
442	11	6.727	13.305
443	10	12.600	19.895
444	15	1.933	4.682
445	15	1.200	1.971
448	17	6.706	6.362
449	13	7.538	11.963
454	4	5.250	6.076
461	12	11.917	12.767
462	11	6.455	8.079
463	15	6.800	7.627
464	7	0.429	0.535
465	12	2.000	2.449
467	17	1.824	3.414
472	5	1.800	3.493
473	15	4.200	6.097
474	19	2.632	3.989
475	4	0.500	0.577
476	15	0.867	2.588
477	16	5.187	19.692
483	18	8.889	8.757
484	11	4.364	7.420
487	13	6.538	8.202
488	20	2.400	4.925
494	8	0.750	1.165
497	8	3.500	6.141
499	15	0.133	0.516
500	6	1.000	1.265

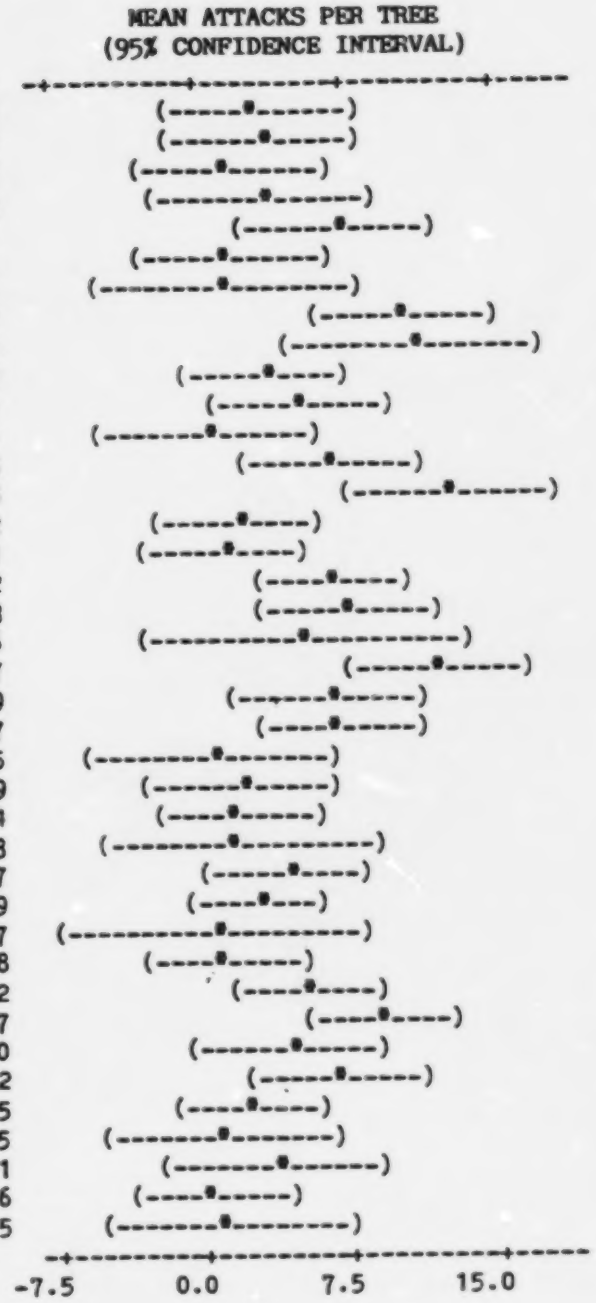

Figure 2: Pityophthorus orarius attack rate by each of 39 clones, Little River Seed Orchard, August, 1985.

nutrients that have been mobilized to nourish expanding reproductive tissues. There are, however, other potential explanations for the phenomenon, such as flowering synchrony or differential survival of beetles in twigs of different nutritional status.

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LITERATURE CITED

Allen, G. S., and J. N. Owens. 1972: The Life History of Douglas-fir. Environment Canada, Forestry Service, Ottawa, Canada.

Anonymous. 1982: SAS User's Guide: Statistics, 1982 Edition. SAS Institute, Inc., Cary, NC.

Anonymous. 1985: Minitab Reference Manual. Minitab, Inc., State College, PA 16801. 209 pp.

Bright Jr., D. E. 1968: Three new species of Pityophthorus from Canada (Coleoptera: Scolytidae). Can. Ent. 100:604-608.

Bright Jr., D.E. 1981: Taxonomic Monograph of the Genus Pityophthorus Eichhoff in North and Central America (Coleoptera: Scolytidae). Memoirs of the Entomological Society of Canada No. 118.

Chamberlin, W. J. 1958: The Scolytoidea of the Northwest: Oregon, Washington, Idaho and British Columbia. Oregon State Monographs, Studies in Entomology No. 2, Oregon State College, Corvallis, Oregon.

Copes, D. 1970: Initiation and development of of graft incompatibility symptoms in Douglas-fir. Silvae Genet. 19:101-107.

Copes, D. 1978: Isozyme activities differ in compatible and incompatible Douglas-fir graft unions. Forest Sci. 24: 2970303.

Daniel, T. W., J. A. Helms, and F. S. Baker. 1979: Principles of Silviculture. McGraw-Hill Book Company, New York. 500 pp.

Hedlin, A. F., and D. S. Ruth. 1970: A Douglas-fir twig mining beetle, Pityophthorus orarius (Coleoptera: Scolytidae). Can. Ent. 102(1), 105-108.

Kramer, P. J. and T. T. Kozlowski. 1979: Physiology of Woody Plants. Academic Press, New York.

Mattson Jr., W. J. 1980: Herbivory in relation to plant nitrogen content. Ann. Rev. Ecol. Syst. 11:119-61.

Ruth, D. S. 1980: A guide to pests in Douglas-fir seed orchards. Can. For. Serv. Pac. For. Res. Cent., Info. Rept. BC-X-204.

Wood, S. L. 1982: The Bark and Ambrosia Beetles of North and Central America (Coleoptera: Scolytidae), a Taxonomic Monograph. Great Basin Naturalist Memoirs, N. 6, Brigham Young University, Provo, Utah.

TECHNICAL SESSION III:

Insect Monitoring and Damage

Moderator: Dr. Harry O. Yates III, Athens, Georgia, USA

EFFECT OF PEST SPECIES EXCLUSIONS ON DOUGLAS-FIR (*PSEUDOTSUGA MENZIESII* [MIRB.] FRANCO) CONE AND SEED INSECTS: IMPLICATIONS FOR PEST MANAGEMENT[1].

by

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SUMMARY

Species exclusions among pests of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) cones were conducted to assess the effect of interspecific competition on pest management in this system. Preliminary results from experimental species exclusions confirmed the hypothesis that pest species populations are not independent of one another. While exclusion of *Megastigmus spermotrophus* had no statistically significant effect on damage by *Contarinia oregonensis*, exclusion of *C. oregonensis* resulted in a highly significant increase in *M. spermotrophus* damage within cones.

Key words: Douglas-fir, seed orchards, competition.

RESUME

Des exclusions des espèces parmis les insectes ravageurs des cônes du sapin de Douglas furent conduites afin d'estimer l'effet de l'action réciproque en compétition entr'espèces sur la ménagement des vergiers à graines. Des exclusions expérimentales des espèces nuisibles ont confirmé l'hypothèse que les densités des populations des insectes nuisibles ne sont pas indépendents l'une à l'autre. Des données préliminaire ont indiqué que

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[1]From a dissertation submitted by the senior author in partial fulfillment of requirements for the Ph. D. degree in Entomology at the University of California, Berkeley, November 1987.

l'exclusion de Megastigmus spermotrophus n'avait aucun effet sur Contarinia oregonensis, mais l'exclusion de C. oregonensis sortait une croissance significative des populations des M. spermotrophus.

Mots-clefs: sapin de Douglas, vergiers à graines, compétition.

INTRODUCTION

In the Pacific Northwest, Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) cones and seeds are fed upon by a complex of insects including the Douglas-fir seed chalcid, Megastigmus spermotrophus Wachtl (Hymenoptera: Torymidae), the Douglas-fir cone gall midge, Contarinia oregonensis Foote (Diptera: Cecidomyiidae), the fir coneworm, Dioryctria abietivorella (Grote) (Lepidoptera: Pyralidae), the Douglas-fir cone moth, Barbara colfaxiana (Kearfott) (Lepidoptera: Tortricidae), and the western conifer seed bug, Leptoglossus occidentalis Heidemann (Hemiptera: Coreidae) (Hedlin et al. 1980). The presence of a complex of pests such as this can greatly complicate pest management because of the potential for species interactions such as competition and predation. It has been speculated that, in such cases, the resource which is protected from one pest species may simply be consumed by a later-arriving species (Annila 1973; Levins and Wilson 1980; Roques and Raimbault 1985), especially if the control method is effective for only a limited period of time. Competitive displacement has long been seen in other crop situations (Flint and van den Bosch 1981), and was predicted for the Douglas-fir cone and seed pest complex almost three decades ago (Koerber 1960). Annila (1973) reported this phenomenon in pests of spruce seed production in Finland, and Mattson (1986) found evidence for the mechanism in two pest species attacking red pine. Given the extended attack phenologies of the pests of Douglas-fir cones, we felt that competitive displacement was also likely, at least in theory, to affect pest management of Douglas-fir cone and seed insects.

There were several reasons why we felt that competition might be important in this group of insects. First, competition is most likely to occur in situations where resources are limiting, and Douglas-fir cones are at least cyclically limiting because abundant cone crops occur at infrequent intervals (Isaac and Dimock 1958; Lowry 1966). Further evidence that resources are limiting for Douglas-fir cone and seed pests is the fact that extended diapause has been seen in all of the major pest species except for D. abietivorella, which relies on spatial rather than temporal escape from competition (Rappaport and Volney 1986).

Second, pest life-histories support the expectation that competition might influence pest population levels in this group of insects, because both predation and displacement appear likely. All of the major pests of Douglas-fir seeds and cones except for Leptoglossus occidentalis have limited vagility as immatures, so they are especially constrained when food resources are limited. We have seen both B. colfaxiana and D. abietivorella feeding on C. oregonensis larvae, and they may also consume M. spermotrophus larvae that they encounter. In these encounters, neither C. oregonensis nor M. spermotrophus has any morphological adaptations for defense. Although M. spermotrophus larvae may be found in C. oregonensis-galled seeds, we have seen this phenomenon only at low midge densities. We have never seen M.

spermotrophus larvae in heavily midge-infested scales. We do not know whether this is because M. spermotrophus fails to oviposit in seeds borne on heavily-infested scales or because M. spermotrophus eggs deposited in C. oregonensis-infested seeds fail to develop. In all of these potential encounters, M. spermotrophus would appear to have the greatest capacity for being displaced or preyed upon.

Third, there is circumstantial evidence for competition in this group of insects in the relative difference in M. spermotrophus population densities in North America, where it exists with competing species (Hedlin et al. 1980, Schowalter et al. 1985), and in Europe, where it is the sole major pest of Douglas-fir seeds (Roques 1983). European chalcid populations are generally much higher than North American populations (Roques 1983). Alternative explanations for this difference, such as differential predation, parasitism, or pathogens in the two continents, are unlikely for several reasons. The North American parasite complex is quite depauperate (Bringuel 1967), and autochthonous parasites in Europe have adapted to M. spermotrophus (Roques 1981). Consequently, levels of parasitism in European M. spermotrophus are actually higher than those in North America. Furthermore, there are, to our knowledge, no pathogens of M. spermotrophus on either continent.

Fourth, evidence from insecticide tests in Douglas-fir seed orchards suggests that pest species may compensate for mortality among coexisting species by expanding into the niche thus provided. Dale and Frank (1981), Koerber and Markin (1984), Stein and Markin (1984), and Summers and Miller (1986) all report instances where treatment of a complex of pests in Douglas-fir resulted in an increase in one of the pest species' population densities even though other species in the complex were controlled. This could be construed as de facto evidence of competitive displacement, although such a conclusion is premature without more rigorous investigation into the mechanism responsible for changes in population density (Hastings 1987). To study this problem, we conducted a species exclusion study to test the hypothesis that species population densities were independent of one another.

MATERIALS AND METHODS

In this study, we focused on the three major pest species which are specific to Douglas-fir and which complete their larval development within the cones, that is, Contarinia oregonensis, Barbara colfaxiana, and Megastigmus spermotrophus. All of these pests had been reported from our study site in a previous survey.

The studies were conducted at the Little River Seed Orchard (operated by Louisiana-Pacific Corporation) in Humboldt County, California. This 6-hectare Douglas-fir seed orchard is about 10 km inland from the Pacific Ocean at an elevation of 91 m. The orchard, which is surrounded by mature redwood and Douglas-fir, originally consisted of 3000 trees (30 ramets each of 100 clones), planted in 1976-1978. Orchard management practices have consisted simply of annual mowing and pruning, and sanitation of cones in most years. At the time of the study, no herbicide, insecticide, or fertilizer treatments had ever been performed in the orchard, which was just then coming into cone production.

To test the hypothesis that species' population densities were independent of one another, we excluded each of the major pest species individually and in combination with each of the others. This scheme constitutes a 2^3 factorial, the factors being presence or absence of C. oregonensis, presence or absence of B. colfaxiana, and presence or absence of M. spermotrophus. There were, consequently, eight different exclusion treatments.

Although there is some overlap in the oviposition phenologies of these three pest species (Volney 1984), there was enough separation of peak oviposition times that species could be manipulated individually. C. oregonensis is the first species in the community to begin ovipositing, and oviposition is closely correlated with conelet pollination (Johnson 1963a). C. oregonensis oviposits while scales are open and conelets are erect. After the scales become appressed, female midges can no longer reach the bases of the scales where eggs must be deposited. Although oviposition by B. colfaxiana begins during the peak oviposition period of the midge, B. colfaxiana oviposition does not peak until midge oviposition is nearly complete (Hedlin 1960). B. colfaxiana oviposition continues until shortly after M. spermotrophus begins to oviposit. In Ukiah, CA, which is inland but about 2° farther south than our study site, M. spermotrophus begins to oviposit in early May, continuing until almost June. The only problematical species combination was C. oregonensis - B. colfaxiana, which in some areas have a few weeks of overlap in their oviposition phenologies. However, we reasoned that cones which were intended to have the cone moth excluded but needed to be exposed for ovipositing midges could be examined each week and the large, easily visible cone moth eggs scraped off the cone surface.

Exclusions were accomplished using fiber pollination bags with clear plastic windows. Each cone-bearing branch was wrapped with cotton to improve the exclosure. Then the bag was placed over the branch, cinched around the cotton, and tied tightly with polyester cord. Color-coded flagging was used to mark treatments. To permit assessment of ramet-to-ramet variation, we attempted to select two ramets per clone for each of four clones (eight trees total). However, the vagaries of cone production forced us to select four clones which had only one highly fecund ramet, one which had two, and one which had three. This scheme still provided us with two clones which had sufficient numbers of ramets to assess between-ramet variation. Trees were divided into two crown levels. The most fecund branches were then selected from each crown level of each tree, and treatments were randomly assigned to those branches. We predicted a maximum abortion rate of about 67%, so 3 times as many cones as ultimately needed were flagged for treatment (i. e. at least 6 cones per treatment at each crown level). All eight exclusion treatments were thus replicated twelve times (6 replicates for each of two crown levels) on each of nine trees.

Cones that were bagged during their normal pollination period (i.e., conelets erect and open) were artificially pollinated with a mixture of pollen from throughout Northern California using a 10-ml disposable plastic syringe coupled with a pipetting bulb and a 1 mm-bore needle (Orr-Ewing 1956). Artifical pollinations were repeated weekly on all cones until they became pendant. At the beginning of August, when all oviposition by pest species was assumed to be complete, all cones were bagged in order to prevent damage to treated cones by L. occidentalis

Mature cones were harvested at the end of the season and dissected (Volney 1984); damage by individual species was documented. The variable of interest was the percentage of the resource consumed by each species for each

treatment. For the seed chalcid, the resource consisted of the sum of sound seeds and infested seeds (Roques 1983). For all other species, the resource consisted of potential seeds (i.e., two time the number of scales) because all can survive whether or not a sound seed is produced. Analysis of variance (SAS Institute 1985) was performed on percent of the resource consumed by each species for each treatment regime. Differences among means were compared using Bonferroni's inequality (Bailey 1977).

RESULTS AND DISCUSSION

As mentioned above, C. oregonensis emerges about the time that conebuds burst, and oviposits on the interior surface of scales in the region where seeds develop. Larvae emerge and penetrate the scale, causing the formation of a gall which diverts nutrients away from the seed and fuses the seed to the scale, rendering the seed unextractable (Hedlin 1961; Johnson 1963b). Larvae feed within these galls throughout the summer and emerge from cones in the fall, then drop to the litter to overwinter.

D. abietivorella apparently oviposits in synchrony with M. spermotrophus at our study site, since it was present only in treatments which were exposed to oviposition by M. spermotrophus. Its life-history is apparently quite variable and is not well known. Eggs are laid on or near cones; larvae hatch, bore into cones, and mine a cylinder around the rachis of the cone, consuming seeds and other tissues. They may be thought of as accidental predators on other cone-inhabiting insects, because we have seen larvae feeding on C. oregonensis larvae within galls that happen to be in their path. Larvae complete development in late summer, then leave the cone to spin cocoons and overwinter in the litter (Hedlin et al. 1980).

M. spermotrophus begins ovipositing around May 1, when cones are about half their mature length, and continues until late June. Oviposition thus extends for about one month before and one month after fertilization of the female gametophyte takes place, which occurs around June 1 at Little River. Larvae hatch and feed on endosperm until late in the season, when they start to consume the developing embryo. Like C. oregonensis, M. spermotrophus larvae are sessile during virtually their entire development and have no obvious morphological adaptations for defense. Thus, we might expect these two species to suffer the greatest displacement in a competitive situation.

Pairwise comparisons between exclusion treatments (Table 1) revealed that C. oregonensis damage was not significantly different in the presence and in the absence of M. spermotrophus and D. abietivorella. This result is not surprising, since it is difficult to conceive of a way in which M. spermotrophus, which is a later-arriving and virtually defenseless species Hussey 1955), could displace C. oregonensis larvae once they have esptablished galls in the scale tissue. The reduction in C. oregonensis damage may be attributable to the presence of D. abietivorella, although this conclusion cannot be proven with the data at hand because D. abietivorella and M. spermotrophus were not assessed separately. On the other hand, exclusion of C. oregonensis from cones resulted in a twofold increase in M. spermotrophus damage, and this difference was highly significant ($P \leq 0.001$, t-test modified for unbalanced design). This result is consistent with what we know about the biologies of these species, and suggests that M. spermotrophus has the potential to become a more serious pest of Douglas-fir

Table 1: Pairwise comparisons between pest species exclusion treatments on Douglas-fir cones, Little River Seed Orchard, 1985 (Procedure-wise error rate $\leq$ 0.05)

Variable=Percentage of resource utilized by *Contarinia oregonensis*:

Grouping	Mean %	N	Treatment
A	5.079	41	Exclude *Megastigmus spermotrophus*
A	2.768	89	Control (no species excluded)

Variable=Percentage of resource utilized by *Megastigmus spermotrophus*:

Grouping	Mean %	N	Treatment
A	23.81	7	Exclude *Contarinia oregonensis*
B	13.58	41	Control (no species excluded)

seed production in North America if we succeed in controlling the early-arriving pest species.

Our results indicate that, in its indigenous region, *M. spermotrophus* appears to be excluded from portions of cones occupied by dipteran and lepidopteran species. Where *M. spermotrophus* was accidentally introduced without competitors, it is fully capable of utilizing this portion of the cone and in fact can destroy as many seeds as does the entire complex in the indigenous region (Roques 1983). The species exclusion study confirmed that, even within a single season, suppression of competitors of *M. spermotrophus* in its indigenous region resulted in a significant increase in chalcid damage (as measured by percentage of sound seeds damaged). These results may explain, in large part, the failure of insecticide treatments to increase seed yield (Stein and Markin 1986, Koerber and Markin 1984).

The implications of these results for pest managment in seed orchards are clear. Although the role of interspecific competition in structuring insect communities is still the subject of much controversy, it has nevertheless been shown, by experimental manipulations such as these, to be important in structuring communities in many circumstances (Schoener 1982). The results from these studies underscore the importance of understanding species' coactions before intitating pest managment, especially in situations where there is a multitude of pest species attacking the resource over a protracted period. Such conditions are fairly common in conifer seed orchards, and similar outcomes should be anticipated whenever one is dealing with a pest complex on a crop for which there is no longrange, broad-spectrum chemical protection.

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LITERATURE CITED

Annila, E. 1973: Chemical control of spruce cone insects in seed orchards. Comm. Inst. For. Fenn. 78:1-25.

Bailey, B. J. R. 1977: Tables of the Bonferroni "t" statistic. J. Am. Stat. Assoc. 72:469-478.

Bringuel, G. J. 1967: A study of the cone and seed insects of Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, in the Santa Cruz Mountains of California. Unpublished Masters thesis, Department of Biology, San Jose State College, San Jose, CA. 103 pp.

Dale, J. W. and C. L. Frank. 1981: Injecting Metasystox-R increases seed yields of large superior Douglas-fir by reducing losses caused by cone insects. Pilot Project Report No. 81-33. USDA Forest Service, Pacific SW Region, Forest Pest Management, 630 Sansome Street, San Francisco, CA 94111.

Flint, M. L. and R. van den Bosch. 1981: Introduction to integrated pest management. Plenum Press, New York. 240 pp.

Hastings, A. 1987: Can competition be detected using species co-occurrence data? Ecology 68: 117-123.

Hedlin, A. F. 1960: On the life history of the Douglas-fir cone moth, Barbara colfaxiana (Kft.) (Lepidoptera: Olethreutidae), and one of its parasites, Glypta evetriae Cush. (Hymenoptera: Ichneumonidae). Can. Ent. 92:826-834.

Hedlin, A. F. 1961: The life history and habits of a midge, Contarinia oregonensis Foote (Diptera: Cecidomyiidae) in Douglas-fir cones. Can. Entomol. 93: 952-967.

Hedlin, A. F., H. O. Yates III, D. Cibrian-Tovar, B. H. Ebel, T. W. Koerber, and E. P. Merkel. 1980: Cone and seed insects of North American conifers. Canadian Forestry Service, United States Dept. Agric. Forest Service, and Secretaria de Agricultura y Recursos Hidraulicos, Mexico (Co-op. Publ., unnumbered). 122 pp.

Hussey, N. W. 1955: The life-histories of Megastigmus spermotrophus Wachtl (Hymenoptera: Chalcidoidea) and its principal parasite, with descriptions of the developmental stages. Trans. R. Ent. Soc. Lond. Pt. 2: 133-151.

Isaac, L. A. and E. J. Dimock II. 1958: Silvical characteristics of Douglas-fir var. menziesii. U. S. Forest Serv. Pacific Northwest Forest and Range Expt. Sta. Silvical ser. 9. 18 pp., illus.

Johnson, N. E. 1963a: Time of attack of the Douglas-fir cone midge in relationship to cone development. Jour. Forestry 61: 350-355

Johnson, N. E. 1963b: Cone-scale necrosis and seed damage associated with attacks by Douglas-fir cone midges. For. Sci. 9: 44-51.

Koerber, T. W. 1960: Insects destructive to the Douglas-fir seed crop in California...a problem analysis. USDA For. Serv. Tech. Paper No. 45, 36 pp.

Koerber, T. W. and G. P. Markin. 1984: Metasystox-R injections increase seed yield of Douglas-fir in California, Oregon, and Washington. IN: Yates, H. O. III, ed., Proceedings IUFRO Cone and Seed Insects Working Party Conference, Athens, GA, pp. 137-146.

Levins, R. and M. Wilson, 1980: Ecological theory and pest management. Ann. Rev. Entomol. 25:287-308.

Lowry, W. 1966: Apparent meteorological requirements for abundant cone crop in Douglas-fir. For. Science 12: 185-192.

Mattson, W. J. 1986: Competition for food between two principal cone insects of red pine, Pinus resinosa. Environ. Entomol. 15:88-92.

Orr-Ewing, A. L. 1956: Controlled pollination techniques for the Douglas fir. Forest Science 2: 251-257.

Rappaport, N. G. and W. J. A. Volney. 1986: Resource utilization by insects colonizing Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) cones. IN: Roques, A., ed., Proceedings Second IUFRO Cone and Seed Insects Working Party Conference, Briancon, France, pp. 157-166.

Roques, A. 1981: Biologie et répartition de Megastigmus spermotrophus Wachtl (Hymenoptera: Chalcidoidea) et des autres insectes liés aux cônes dans les peuplements forestiers et vergers à graines français de sapin de Douglas Pseudotsuga menziesii [Mirb.] Franco. Acta Oecologica Oecol. Applic. 2:161-180.

Roques, A. 1983: Les insectes ravageurs des cônes et graines de conifères en France. Institut National de la Recherche Agronomique, 149 rue de Grenelle, 75341 Paris, France. 150 pp.

Roques, A. and J.-P. Raimbault. 1985: Potentialités déstructrices des insectes ravageurs dans les vergers à graines de Douglas du Lot. R. F. F. 37:26-32, pub. Station de Zoologie Forestière, Centre de Recherches Forestières (I.N.R.A.), Ardon 45160 Olivet, France.

SAS Institute, Inc. 1985: SAS User's Guide: Statistics. 1985 Edition, SAS Institute, Cary, NC. 584 pp.

Schoener, T. W. 1982: The controversy over interspecific competition. Amer. Sci. 70:586-595.

Schowalter, T. D., M. I. Haverty, and T. W. Koerber. 1985: Cone and seed

insects in Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, seed orchards in the western United States: distribution and relative impact. Can. Entomol. 117:1223-1230.

Stein, J. D. and G. P. Markin. 1986: Evaluation of four chemical insecticides registered for control of the Douglas-fir cone gall midge, Contarinia oregonensis (Diptera: Cecidomyiidae), and the Douglas-fir seed chalcid, Megastigmus spermotrophus (Hymenoptera: Torymidae), in Douglas-fir seed orchards. Can. Entomol. 118:1185-1191.

Summers, D. and G. E. Miller. 1986: Experience with systemic insecticides for control of cone and seed insects in Douglas-fir seed orchards in coastal British Columbia, Canada. IN: Roques, A., ed., Proceedings Second IUFRO Cone and Seed Insects Working Party Conference, Briancon, France, pp. 267-283.

Volney, W. J. A. 1984: Competition and survival among insects colonizing Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) cones. IN: Yates, H. O. III, ed., Proceedings IUFRO Cones and Seed Insects Working Party Conference, Athens, GA. pp 77-84.

INVENTORY MONITORING AS A MEANS OF ASSESSING INSECT IMPACT ON DOUGLAS-FIR SEED PRODUCTION IN WESTERN OREGON

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ABSTRACT

Inventory monitoring can improve orchard seed production by indicating the relative losses to various mortality agents and the potential efficacy, in terms of seed production, of control tactics. Our use of inventory monitoring in a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seed orchard has shown that percentage loss of at least 5% (62 kg) of potential seed production to insects during a good cone year amounted to $65,000. We also have been able to implicate early-season damage by a conelet-feeding weevil, *Lepesoma lecontei* (Casey), as a major factor influencing seed production, accounting for 40 - 70% of losses to insects. The major category of loss has been unexplained developmental failure. While much of this loss may reflect inadequate pollination or developmental aberration, our studies have shown that early-season feeding by western conifer seed bugs, *Leptoglossus occidentalis* Heidemann, causes indistinguishable developmental failure. Data presented here indicate that even modest reductions in seed losses to insects could have considerable economic benefit.

Keywords: cone and seed insects, *Contarinia oregonensis*, *Megastigmus spermotrophus*, *Lepesoma lecontei*, *Leptoglossus occidentalis*, seed orchard, pest management.

INTRODUCTION

Inventory monitoring is a process whereby seed orchard managers monitor losses of potential seed to various mortality factors during seed development. This process was pioneered in the southern U.S. where it has proven effective for predicting seed production and improving seed production efficiency (Bramlett and Godbee 1982, Bramlett 1984). Inventory monitoring techniques recently have been introduced in the Pacific Northwest and other regions (Bartram et al. 1983, de Groot 1986, Dombrosky and Schowalter 1988, Shearer 1984).

Inventory monitoring in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seed orchards has been used to assess the relative importance of various seed mortality factors and has led to discovery of previously unrecognized factors. Dombrosky and Schowalter (1988) and Schowalter (1986) reported substantial losses (6-9%) of potential seed to a conelet-feeding weevil, *Lepesoma lecontei* (Casey). Conelet mortality resulting from weevil feeding previously had been ascribed to frost damage. Other mortality factors are likely to be recognized as seed orchard distribution and management practices change through time.

A rich guild of insects is known to reduce seed yields in Douglas-fir seed orchards. Major species in the Pacific Northwest include the Douglas-fir cone gall midge, *Contarinia oregonensis* Foote, the Douglas-fir seed chalcid, *Megastigmus spermotrophus* (Wachtl.), the Douglas-fir cone moth, *Barbara colfaxiana* (Kearfott), and the fir coneworm, *Dioryctria abietivorella* (Groté) (Hedlin et al. 1981, Schowalter et al. 1985). The western conifer seed bug, *Leptoglossus occidentalis* Heidemann, and the western spruce budworm, *Choristoneura occidentalis* Freeman, are known to feed on Douglas-fir cones and seeds, but impacts have not been studied west of the Cascades (Hedlin et al. 1981, Miller 1986c, Schowalter 1986, Shearer 1984).

The purpose of this paper is to describe the use of inventory monitoring to assess the impact of insects on Douglas-fir seed production in western Oregon. The goal of our studies is to relate impacts to changes in cone crop size, environmental conditions, or management practices in order to improve seed production efficiency in Douglas-fir seed orchards.

METHODS

In 1983, we conducted a preliminary study to relate cone gall midge abundance to seed loss. We collected 102 cones from six Douglas-fir seed orchards in western Oregon and Washington during June and July. These cones were sliced axially, and the numbers of infested scales and cone gall midge larvae were recorded. One-half of each cone was dissected completely. The 3-4 infertile scales at each end were discarded. The remaining scales were peeled from the cone and arranged in order from proximal to distal. The scales were divided into three equal strata

(proximal, middle, and distal), and the number of midge larvae in each stratum was recorded. The number of scales, infested scales, and midge larvae was recorded for each cone. Regression techniques were used to identify variables with the greatest value for predicting number of infested scales.

During our initial studies at the Beaver Creek Seed Orchard in western Oregon during 1983, we noted substantial chewing damage to conelets during the flowering period in April. Subsequently, in 1984, we began a monitoring program during March, prior to budbreak, as described by Dombrosky and Schowalter (1988). A poor cone crop was produced during 1984, so our study was limited to 10 of the 25 trees producing cones (of a total of 2250 trees) at Beaver Creek. The crowns of the trees were divided into upper, middle and lower strata, which were sampled separately using methods developed by Miller (1986a). Potential cone production was estimated from cone counts on six whorl branches in each crown stratum of each tree at the flowering stage (April), pendant stage (June), and mature stage (September). Mature cones were dissected to measure seed potential and loss to various factors.

A good crop was produced at Beaver Creek during 1985. About 75% of the trees produced a harvestable number (> 50) of cones. Twenty trees were selected by computer generation for inventory monitoring. Upright conelets were collected in April from the three crown strata of these trees. Conelets were dissected under a microscope and the number of scales and midge eggs was recorded. We subsequently monitored these trees as described above.

During 1985, and as part of continuing studies, we used caging and survey techniques to assess seed losses to two poorly-known insects, the weevil and the western conifer seed bug, in order to provide information on distribution and feeding damage of these insects. Techniques were described by Schowalter (1986).

RESULTS

The 1983 cone dissections indicated that the total number of midge larvae in a cone is the best predictor of percent of scales infested. The equation:

$$\% \text{ infested scales} = -0.3 + \ln(\text{total midges})^{0.2}$$

was highly significant ($P < 0.001$, $R^2 = 0.71$). The non-linear relationship (Figure 1) indicated that a relatively small number of midges occupy all suitable scales. Additional midges caused little additional damage. Each infested scale harbored an average of 4.4 ($\pm$ 2.1) midge larvae, enough to cause loss of both seeds on the scale.

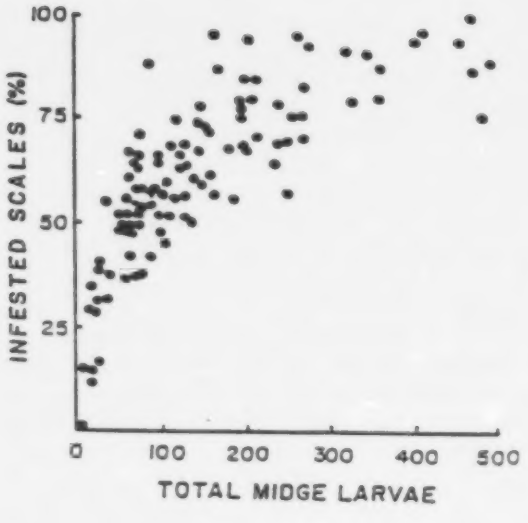

Figure 1. Percent of scales infested relative to total Douglas-fir cone gall midge larvae in cones from western Oregon and Washington in 1983. N = 102.

Table 1. Fate of potential seed at Beaver Creek Seed Orchard in western Oregon during 1984 (a poor crop year) and 1985 (a good crop year).

	1984		1985	
Seed Category	kg	%	kg	%
Potential Seed	20	100	1235	100
Cone Mortality				
Weevil	1.8	9	74	6
Frost	2.6	13	49	4
Seed Mortality				
Developmental Failure	12	58	642	52
Cone Gall Midge	1.6	8	24	2
Seed Chalcid	1.0	5	12	1
Other Factors[1/]	0.6	3	12	1
Seed Yield	0.8[2/]	4	420[3/]	34

1/ includes losses to Douglas-fir cone moth, fir coneworm and western conifer seed bug.

2/ from Dombrosky et al. (1988), adjusted to 25 cone-producing trees and assuming 75,000 seed/kg.

3/ actual seed production (W. K. Randall, pers. comm.).

The most widely used predictor of the number of infested scales is the number infested on the exposed axial slice (Miller 1986c). Our data indicated a highly significant relationship ($P < 0.001$):

infested scales = 7.3 + 1.3 x infested scales exposed,

but the R^2 was only 0.48, indicating relatively poor predictive value.

As reported by Miller (1986a) and Rappaport and Volney (1986), midge larvae were most abundant in the middle third of the cone. About 45% of the total larvae were found in this zone. Accordingly, the total midge number was highly correlated ($P < 0.001$, $R^2 = 0.88$) with midge number in the middle third as described by the equation:

total midges = 2.3 + 2.2 x midges in middle third.

Results of inventory monitoring of seed production during 1984 (a poor crop year) and 1985 (a good crop year) are shown in Table 1. Losses to the weevil rank relatively high, compared to other factors, during both years. Apparent losses to insects amounted to 25% of the potential seed during 1984 and 10% during 1985. However, the greatest loss (> 50%) in both years was to unexplained developmental failure (abortion), as observed at other seed orchards in the Pacific Northwest (Schowalter et al. 1985). These data suggest that roughly half of the insect-damaged seed likely would have failed to develop even in the absence of insects (Miller 1986b, c). Nevertheless, at $1,100/kg seed, losses to insects were worth at least $65,000 in 1985.

The low loss of seed to the cone gall midge in 1985 was predictable from egg densities in conelets. Only 20% of the conelets in the upper-crown, and 7% each in the middle and lower strata contained midge eggs (egg density = 2.7/cone, 0.04/cone, and 1.4/cone, respectively). At these low levels, number of eggs was not correlated significantly with number of conelet scales, nor was galled seed at harvest correlated with egg density in conelets, as reported by Miller (1986b).

The relatively high and consistent seed losses resulting from weevil feeding are cause for concern. The distribution of this weevil among Douglas-fir seed orchards is not known, although we have received specimens from orchards in Cottage Grove, Oregon and Centralia, Washington. The life history of this weevil and its preferred hosts also are unknown, although other members of the genus *Lepesoma* (= *Dyslobus*) feed on roots (primarily of Rosaceae) as larvae (Van Dyke 1933).

Our surveys have shown that adults appear in late February. Abundance peaks and feeding on cones begins at the time of bud expansion in March. Cone buds appear to be preferred, although feeding on pollen cones and needles has been observed (Schowalter 1986). Seed loss to weevils in 1985 was associated with densities of 3 ($\pm$ 2) weevils per distal meter of lower whorl branch (Schowalter 1986). We currently are examining relationships between weevil abundance and cone production.

The high seed loss to unexplained developmental failure also warrants scrutiny. This loss has been ascribed to inadequate pollination or developmental aberration, but was consistantly high (> 50%) during both good and poor crop years at Beaver Creek where pollen production by adjacent stands is considerable.

We found that seeds from conelets caged in May with seed bug adults or second instar nymphs were indistinguishable from those ascribed to unexplained developmental failure. About 25% of the conelets caged with adult seed bugs were aborted, compared to no abortion in control cages. Surviving cones in both adult and nymph cages were undersized. Developmental failure in these cones approached 100% at adult densities of 0.2/cone, and nymph densities of 0.8/cone, compared to abortion range of 15-30% in control cages (Figure 2). In other words, estimating seed loss to seed bugs at harvest will underestimate impact, depending on the extend to which seed bugs feed on conelets.

We have not completed studies of seed losses in more mature cones exposed to seed bug feeding. However, we surveyed seed bug density and damage detectable by X-ray (Koerber 1963) in three seed orchards in western Oregon in late August 1983. Seed bug damage was significantly related ($P < 0.02$, $R^2 = 0.86$) to seed bug density (Figure 3), as described by the equation:

$$\% \text{ damage by seed bug} = 0.8 + 32 \times \text{seed bug density}.$$

Although these data indicate that seed loss to seed bugs may be predictable, we obviously need information from more seed orchards and years to increase the range of predictability. We also need information on seasonal distribution and abundances of seed bugs in order to evaluate and predict overall impacts on seed production.

DISCUSSION

Inventory monitoring has a number of practical uses (Bramlett and Godbee 1982, Bramlett 1984). First, it provides a means of assessing factors contributing to seed losses. For example, our studies have shown that unexplained developmental failure and *L. lecontei* are the two most consistent loss factors at Beaver Creek. The role of the weevil might have continued to be unrecognized without the use of inventory monitoring. Second, inventory monitoring permits cost analysis of seed production. At $1,100/kg for Douglas-fir seed, losses to insects at Beaver Creek amounted to at least $3,000 in 1984 and at least $65,000 in 1985, depending on the amount of insect-damaged seed that would have failed to develop in the absence of insects. Third, given appropriate experimental controls and adequate replication, inventory monitoring could provide the means to assess the effectiveness of management practices that control mortality factors (Miller 1983). If losses to insects could be reduced, seed production efficiency could be improved substantially.

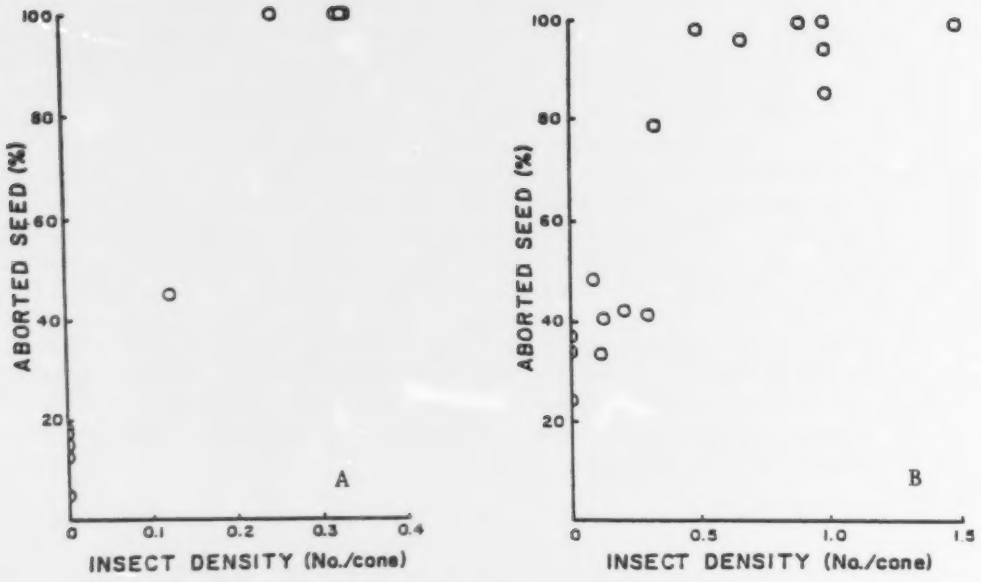

Figure 2. Seed loss relative to density of western conifer seed bug adults (A) and nymphs (B) in cages in a Douglas-fir seed orchard in western Oregon.

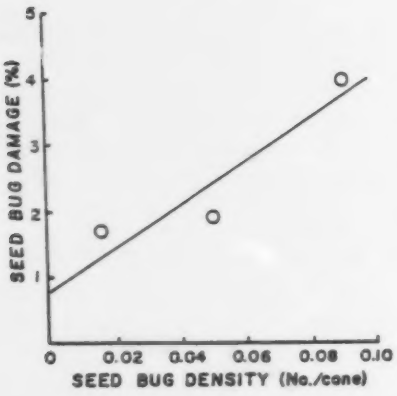

Figure 3. Seed bug damage to Douglas-fir seed as a function of seed bug density for three seed orchards in western Oregon.

Although inventory monitoring can be used to assess the importance of mortality factors, its use requires reliable sampling techniques and adequate information on causes of seed loss. Sampling is particularly important in providing information on the extent and distribution of losses (Bramlett and Godbee 1982, Bramlett 1984). Dombrosky and Schowalter (1988) reported that during a poor cone year, at least 12 cones from 100 trees might be necessary to assess losses to the most important factors (developmental failure, cone mortality, cone gall midge and seed chalcid) at a 0.2 standard error level of precision. However, our data for 1985, a good cone year, indicate that 100 cones would be sufficient for this level of precision, as also found by Miller (1986a). Miller (1986b) developed a sequential sampling system for evaluating cone gall midge impact in seed orchards in British Columbia. All of these studies have indicated the importance of collecting cones throughout the crown. Orchard managers must determine the suitability of sampling procedures based on the required precision and cost of sampling (Miller 1983).

Improved seed production efficiency requires better information on causes of seed losses. Losses may not be due to the most apparent factor. For example, damage caused by the cone weevil, *L. lecontei*, frequently has been ascribed to frost damage. The factors responsible for the substantial losses to unexplained developmental failure are not well known. Although pollination and developmental aberrations are likely factors, our implication of seed bugs as a possible cause warrants further investigation into the extent of seed bug feeding and damage to cones and seeds. The data presented here indicate that even modest reduction in loss of Douglas-fir seed to insects could provide considerable economic return.

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LITERATURE CITED

Bartram, C., G. E. Miller, C. Leadem and H. Rooke. 1983. Quantification of orchard seed production efficiencies and absolute seed losses from the time of flowering through germination: progress report for 1982. Seed Orchard Management Study SX 82609-Q, B.C. Ministry of Forests, Victoria.

Bramlett, D. L. 1984. Inventory-monitoring system for southern pine seed orchards. pp. 102-111, In: H.O. Yates III, ed., Proced. of the cone and seed insects work party conf. IUFRO Working Party S2.07-01. U.S.D.A. SE For. Exp. Stn., Asheville, NC.

de Groot, P. 1986. Mortality factors of jack pine, *Pinus banksiana* Lamb., strobilli. pp. 39-52, In: A. Roques, ed., Proced. of the 2nd conf. of the cone and seed insects working party. IUFRO Working Party S2.07-01. Inst. National Recherche Agron., Ardon, France.

Dombrosky, S. A. and T. D. Schowalter. 1988. Inventory monitoring for estimating impact of insects on seed production in a Douglas-fir seed orchard in western Oregon. J. Econ. Entomol. 81: 281-285.

Hedlin, A. F., H. O. Yates III, D. C. Tovar, B. H. Ebel, T. W. Koerber and E. P. Merkel. 1981. Cone and seed insects of North American conifers. Can. For. Serv./U.S.D.A. For Serv./Secr. Agric. Recur. Hidraul, Mexico. Victoria, B.C.

Koerber, T. W. 1963. *Leptoglossus occidentalis* (Hemiptera: Coreidae), a newly discovered pest of coniferous seed. Ann. Entomol. Soc. Am. 56: 229-234.

Miller, G. E. 1983. When is controlling cone and seed insects in Douglas-fir seed orchards justified? Forestry Chron. 59: 304-307.

Miller, G. E. 1986a. Distribution of *Contarinia oregonensis* Foote (Diptera: Cecidomyiidae) eggs in Douglas-fir seed orchards and a method for estimating egg density. Can. Entomol. 118: 1291-1295.

Miller, G. E. 1986b. Damage prediction for *Contarina oregonensis* Foote (Diptera: Cecidomyiidae) in Douglas-fir seed orchards. Can. Entomol. 118: 1297-1306.

Miller, G. E. 1986c. Sampling major Douglas-fir cone and seed insects in British Columbia. pp. 103-112, In: A. Roques, ed., Proced. of the 2nd conf. of the cone and seed insects working party. IUFRO Working Party S2.07-01. Inst. National Recherche Agron., Ardon, France.

Rappaport, N. G. and W. J. A. Volney. 1986. Resource utilization by insects colonizing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) cones. pp. 157-166, In: A. Roques, ed., Proced. of the 2nd conf. of the cone and seed insects working party. IUFRO

Working Party S2.07-01. Inst. National Recherche Agron., Ardon, France.

Schowalter, T. D. 1986. *Lepesoma lecontei* (Coleoptera: Curculionidae): an agent of conelet abortion in a Douglas-fir seed orchard in western Oregon. J. Econ. Entomol. 79: 843-846.

Schowalter, T. D., M. I. Haverty and T. W. Koerber. 1985. Cone and seed insects in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seed orchards in the western United States: distribution and relative impact. Can. Entomol. 117:1223-1230.

Shearer, R. C. 1984. Influence of insects on Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, and western larch, *Larix occidentalis* Nutt., cone and seed production in western Montana. pp. 112-121, In: H.O. Yates III, ed., Proced. of the cone and seed insects work party conf. IUFRO Working Party S2.07-01., U.S.D.A. Forest Service SE For. Res. Stn., Asheville, NC.

Van Dyke, E. C. 1933. A short review of *Dyslobus* LeConte, a genus of broad-nosed weevils of the subfamily Otiorhynchinae with descriptions of new species. Pan-Pac. Entomol. 9:31-47.

SEED COUNTS AND CONE INSECT FORAGING DAMAGE IN RELATION TO CONE-COLLECTION DATE AND STAND TYPE IN WHITE SPRUCE

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ABSTRACT

White spruce Picea glauca (Moench) Voss. cones were sampled at periodic intervals until cone maturation (June 4 to July 30) in three different stand types (plantations, open stands, mixed stands) to find (a) the most appropriate time to assess cones for determining sound seed yields and identifying insect damage, and (b) to assess the influence of stand type on cone insect foraging activities and production of sound seeds. For three of the most destructive insects, damage to cones reached a maximum early or midway through the sampling period and, thereafter, declined. The number of sound seeds decreased steadily over the course of the summer but appeared to reach a minimum level by mid-July. Some insects are more sensitive than others to stand type.

Keywords: White spruce, Picea glauca, cone and seed insects, cone-collection date, stand type.

RÉSUMÉ

Des cônes d'épinette blanche (Picea glauca [Moench] Voss.) ont été prélevés à des intervalles réguliers jusqu'à ce qu'ils soient matures (du 4 juin au 30 juillet) dans trois types différents de peuplements (plantations, peuplements clairs et peuplements mixtes). On voulait déterminer le moment d'évaluation des cônes le plus approprié pour l'établissement du rendement en graines saines ainsi que l'appréciation des dommages causés par les insctes et étudier l'influence du type de peuplement sur l'activité alimentaire d'insectes déprédateurs des cônes et la production de graines saines. Les dommages causés aux cônes par les insectes ont atteint un maximum au début ou au milieu de la période de prélèvement des cônes et ont diminué par la suite pour trois des insectes les plus destructeurs. Le nombre de graines saines a diminué de façon constante pendant l'été, mais a semblé atteindre un niveau minimal vers la mi-juillet. Certains insectes ont été trouvés sensibles au type de peuplement, d'autres, non.

Mots-clés: épinette blanche, Picea glauca, insectes ravageurs des cônes et des graines, date de récolte des cônes, type de peuplement.

INTRODUCTION

Insect foraging on cones and seeds is a major factor contributing to seed losses of white spruce Picea glauca (Moench) Voss (Tripp and Hedlin 1956). An important means of dealing with these losses is to carry out a reconnaissance survey to assess the seed yield of cone crops prior to operational collections; if predicted seed yields are below an acceptable level, cones are simply not collected (Dobbs et al. 1976). Seed yields are assessed by counting the number of sound seeds on longitudinal sections of cones. This, plus an assessment of rates of cone infestation by insects, is also used to evaluate the efficacy of insecticide treatments (Fogal and Plowman 1988).

The reliability of the seed counts and insect damage assessments is likely to depend upon the time of cone sampling; potential seed yields will be overestimated if sound seeds are counted before all losses occur and cone- infestation rates will be underestimated if cones are examined before all insect damage has occurred. The latter problem is complicated by the fact that several insects feed on white spruce cones (Tripp and Hedlin 1956). Thus, one aim of this study was to find the most appropriate time to assess white spruce cones for sound seed yields and for identifying insect damage and seed losses.

Stand type influences the proportion of white spruce cones damaged by insects (Fogal et al. 1977). It may also influence pollination success, selfing, seed development, and the proportion of potential seeds that develop to maturity (Owens and Blake 1985). Therefore, a second aim of this study was to assess the influence of stand type on cone insect foraging activities and the production of sound seeds.

MATERIALS AND METHODS

Insect damage to cones and fate of seeds were investigated in cones from trees in three forest cover types (12 plantations, 11 open stands, and 13 mixed stands). All open and mixed stands were located on private or crown land within a 25-km wide strip along the south shore of the Ottawa River between the Chalk River and the Bonnechere River tributaries. Plantations were clustered near Chalk River, Ontario on land administered by the Petawawa National Forestry Institute and the Department of National Defence. Characteristics of the three stand types are given in Table 1.

A seed-cone bearing tree was chosen on May 18, 1981 at the peak of flowering in each sample stand of each cover type. The average ages, heights, and diameters of typical sample trees in each stand type, as determined in 1983, were as follows: plantations, 27.9±3.4 years, 10.4±1.4 m, and 15.0±1.3 cm; open stands, 45.3±2.8 years, 14.2±9.7 m, and 29.4±2.4 cm; mixed stands, 45.5±3.6 years, 15.0±0.7 m, and 22.8±1.4 cm. Ten cones were collected from each tree on June 4, 15, 24, July 2, 14, and 30, 1981. The presence of insects or the occurrence of insect damage was determined for each cone as described elsewhere (Fogal et al. 1987). Damage by the following insects was noted: budworm Choristoneura fumiferana (Clemens); coneworm Dioryctria reniculelloides Mutuura and Munroe; spruce seedmoth Cydia youngana (Kearfott); spruce cone maggot Lasiomma anthracina (Czerny); and spruce cone axis midge Dasineura rachiphaga Tripp. Seed-chalcid or seed-midge larvae within seeds,

were recorded as seed-inhabiting insects. All of the exposed sound seeds (those containing a well-developed gametophyte) on the face of one section were then counted.

Table 1. Characteristics of white spruce stands and sample trees used for collecting cones to assess cone insect damage and fate of seeds.

	Plantations	Open stands	Mixed stands
Number of stands	12	11	13
Basal area (m^2/ha)			
Hardwoods	0.6 ±0.6	2.7 ±2.7	12.9 ±4.0
Conifers	31.7 ±4.5	22.1 ±5.4	27.7 ±5.5
White spruce (all)	31.4 ±4.0	19.6 ±5.5	15.7 ±4.0
White spruce (<10cm)	5.6 ±2.3	0.1 ±0.1	1.0 ±0.4
White spruce (>10<20)	17.8 ±4.2	2.1 ±1.1	2.1 ±1.0
White spruce (>20 cm)	8.0 ±4.1	17.4 ±5.4	12.6 ±4.0
All trees	32.3 ±4.4	24.9 ±5.5	40.6 ±6.3
Stems/Ha			
Hardwoods	567 ±361	164 ±75	3092 ±486
Conifers	2683 ±657	618 ±95	1846 ±486
White spruce (all)	2633 ±658	436 ±70	523 ±151
White spruce (<10 cm)	1283 ±468	137 ±84	246 ±88
White spruce (>10<20)	1183 ±293	91 ±41	123 ±58
White spruce (>20 cm)	167 ±81	236 ±65	154 ±40.2
All trees	3250 ±663	782 ±95	4938 ±614
Canopy height (m)	10.6 ±1.2	13.4 ±0.8	14.9 ±0.4
Forest site class	4.3 ±0.1	3.6 ±0.3	3.8 ±0.2

To equalize variances per cent cone damage values were transformed to arc sine $\sqrt{\%}$ before analyses. Seed counts were not transformed. Treatment effects were tested by analyses of variance (Steel and Torrie 1960).

RESULTS

A preliminary two-way analysis of variance to compare effects of stand type and collection date revealed highly significant differences among collection dates for all insects examined and for seed counts (Table 2). Differences among stand types were evident for per cent cones damaged by each insect, except the coneworm. Stand type and collection date interactions were significant for per cent cones damaged by seedmoth and seed midge/ chalcid and sound seed. Therefore, comparisons of collection date are considered separately for each stand type.

Table 2. F-values for effects of stand type (plantations, open stands, mixed stands), collection date and interactions of stand type and collection date for per cent cones damaged by insects and seeds per cone section.

	ANOVA F-Values		
	Stand type	Collection date	Stand type x collection date
Per cent cones damaged by			
Budworm	18.83**	4.64**	1.08
Coneworm	0.31	7.89**	0.40
Seedmoth	97.73**	36.91**	7.43**
Cone maggot	10.84**	3.69**	1.63
Cone-axis midge	2.56*	9.32**	1.12
Seed inhabitants	3.74*	24.08**	2.96**
Sound seed	1.22	97.04**	3.27**

* ($P < 0.05$) or ** ($P < 0.01$).

Damage by budworm was evident on the first sampling date in each stand type. The amount of cone damage ranged from a low of 2% to a high of 35% and tended to be lower in the plantations compared with open stands and mixed stands. The percentage of cones damaged tended to increase to the second, third or fourth collection date and then to decline. Coneworm damage was not evident until the second sampling date and tended to increase through the season to a high of 22% of cones damaged. There were no differences among stand types. Damage to cones by seedmoth appeared in very low proportions on the first sampling date. It reached a maximum by the second sampling date and remained unchanged throughout the ballance of the season, except in open stands where it appeared to decline somewhat by the last sampling date. The proportion of cones damaged was highest in open stands, lower in mixed stands and lowest in plantations. Cone maggot damage was evident at all sampling dates, peaking at the first or second sampling and thereafter declining in open stands and in mixed stands; no decline occurred in plantations. The proportion of cones damaged was relatively high in all stand types but tended to be lower in old fields compared to plantations and mixed stands. Damage by the cone-axis midge was first recorded at the fifth sampling date (July 14) in all stand types and did not increase beyond 10%. Damage by seed-inhabiting insects (seed midge or seed chalcid) was first recorded at the third or fourth sampling date. The proportion of damaged cones did not increase beyond 20%.

Marked reductions in sound seed were observed over the season, decreasing from a high of 18 per cone section at the first sampling date to a low of 2 seeds per cone section by July 30. The numbers of sound seeds appeared to reach a minimum by July 14 with no further reduction at July 30, the last sampling date in open and mixed stands. No differences among stand types were evident when all sampling dates were included in the analysis.

DISCUSSION

The time between seed-cone maturation (late July to early August) and seed fall (mid-Septemer) in white spruce is relatively short and varies annually, making cone and seed collection programs difficult to schedule. A delay of even one day in commencing collections can result in a lost collection and thus a shortage of seed for regeneration (Waldron 1965). Cones of white spruce cease growing after embryo fertilization (Rauter and Farrar 1969) and it is possible to collect white spruce cones as early as August 1 and ripen them artificially in cold storage (Winston and Haddon 1981). If cones are collected early, estimates of potential seed yields also need to be done early. However, results of this study indicate that sound seeds reached a minimum number between mid- and late July so that counting sound seeds prior to mid-July would have given overestimates of potential seed yields. The choice of time for estimating insect damage is complicated by the change in proportions of cones damaged during the summer. For budworm, cone maggot, and seed moth, there is a reduction in proportion of damaged cones following a peak in mid-season. This suggests that cones damaged by these insects may drop early, enriching the proportion of healthy cones on the tree. Premature cone abscission is common in conifers and insect feeding is considered to be one of the factors responsible (Owens and Blake 1985). Waiting until late July to assess cone damage by these insects during the year of this study would have resulted in underestimates of damage. However, damage by the cone-axis midge and seed-inhabiting insects did not become evident until late July and seed losses didn't reach a maximum until then. As a compromise, assessments could be made no earlier than mid-July to ensure that late-damaging insects are identified and that seed losses are close to maximum. If time permits, two to three samples over the course of the summer would alleviate uncertainties.

Foraging activity by cone and seed insects as measured by the proportion of cones damaged and seed losses varies with size of the cone crop (Werner 1964). In the year of this study, foraging activity was influenced by stand type, perhaps because of differences in biological or physical features of the stands on development and/or behavior of the insects. It appears that some of the spruce insects are more sensitive than others to differences in stand type. The seedmoth foraged most heavily in open stands, less in mixed stands, and very little in plantations. The cone maggot caused high cone damage in all stands but tended to forage less frequently on cones in open stands. Spruce budworm, cone-axis midge, and seed-inhabitants were slightly sensitive to stand differences. Foraging by coneworm did not differ among stands.

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REFERENCES

Dobbs, R.C., D.G.W. Edwards, J. Konishi and D. Wallinger. 1976. Guidelines to collecting cones of B.C. conifers. British Columbia Forest Service/ Canadian Forestry Service, Joint Report No. 3.

Fogal, W.H., S.M. Lopushanski and B.D. Haddon. 1977. Insects attacking white spruce cones in three habitats. Proc. Entomol. Soc. Ont. 108:5.

Fogal, W.H. and V.C. Plowman. 1988. Field trials of systemic insecticides for protecting northern spruce and pine seeds trees. In Kielbaso, J. et al., eds. Proc. Second Symp. Systemic Chemical Treatments in Tree Culture. The Kellogg Centre for Continuing Education, Michigan State University, East Lansing, Michigan, Oct. 5-7, 1987. In prep.

Fogal, W.H., S.M. Lopushanski, D.A. MacLeod and D.A. Winston. 1987. Soil incorporation of carbofuran for protecting black spruce seed trees from insects. Proc. Entomol. Soc. Ont. In Press.

Hedlin, A.F., H.O. Yates, D.C. Tovar, B.H. Ebel, T.W. Koerber and E.P. Merkel. 1980. Cone and seed insects of North American conifers. Environ. Can., Can. For. Serv./USDA Forest Serv./Sec. Agric. Recur. Hidraul., Mexico. Victoria, B.C.

Owens, J.N. and M.D. Blake. 1985. Forest tree seed production. A review of the literature and recommendations for future research. Can. For. Serv. Inf. Rep. PI-X-53.

Rauter, R.M. and J.L. Farrar. 1968. Embryology of Picea glauca (Moench) Voss. Proc. 16th Northeastern Forest Tree Improv. Conf., Macdonald College, Montreal, Quebec. Aug. 1968. pp. 13-24.

Steel, R.G.D. and J.H. Torrie. 1960. Principles and Procedures of Statistics. McGraw-Hill Book Co. Inc., New York.

Tripp, H.A. and A.F. Hedlin. 1956. An ecological study and damage appraisal of white spruce cone insects. For. Chron. 32:400-410.

Waldron, R.M. 1965. Cone production and seedfall in a mature white spruce stand. For. Chron. 41:316-329.

Werner, R.A. 1964. White spruce seed losses by insects in interior Alaska. Can. Entomol. 96:1462-1464.

Winston, D.A. and B.D. Haddon. 1981. Effects of early cone collection and artificial ripening on white spruce and red pine germination. Can. J. For. Res. 11:817-826.

The Spatial Structure of Populations and Measure of Aggregation and Sampling of Cone and Seed Insects

by

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It is difficult to obtain the precious information about the abundance of cone and seed pests with the purpose of damage prognosis and the expediency of protective measures because of uneven distribution of cones in crowns, periodicity of fruiting, endophytious life of conobionts and unevenness of distribution of their larvae. Hence, during working out the sampling plans and realization of inspective and protective measures we must take in consideration the features of spatial structure of pest populations. This problem remains scantily explored, in contrast to exophytious insects.

The peculiarities of spatial distribution (SD) of conobiotious larvae are, firstly, the extremely high degree of its discreteness (Stadnitzky, Bortnik, 1977) and, secondly, little acceptability of non-sample methods of its study. So, that methods as the analysis of distances between the individuals (Odum, 1983), altitudes of localization above ground-surface, etc., have low acceptability in forest conditions. Hence, it is most suitable to approximate the SD of conobiotious larvae on the basis of numbers-distribution in series of samples, analogically to exophytious insects (e.g., Harcourt, 1963, 1965, Taylor, 1984). Different indices of aggregation (homogeneity) were developed for the rapid evaluation of the character of SD. Among the last the indices of dispersion ($A_1 = \frac{\sigma^2}{\bar{x}}$), Lloyd's mean crowding $A_2 = \frac{\bar{x}^2 + \sigma^2 - \bar{x}}{\bar{x}}$ and Moore's ($A_3 = 2\, n_o n_2 / n_1^2$) can be marked out, where $\bar{x}$ - the mean number of individuals per sample (population density), σ^2 - dispersion, and n_o, n_1, n_2 - frequencies of samples with nul, one and two individuals respectively. It is known (Mirkin, Rosenberg, 1983), that the SD is aggregated with $A_1 > 1$, $A_2 >> 1$ and $A_3 >> 1$. In other cases the SD is either random (when $\sigma^2 = \bar{x}$), or regular (when $\sigma^2 < \bar{x}$) (Odum, 1983).

The aim of this publication was evaluation of indices A_1, A_2 and A_3 referring to cone-damaging insects on the bases of many years materials and the comparing of their variability with the needs of inspective egg countings.

Because of distinct fruiting periodicity of European fir the authors in some years had very scanty excerpts: in the years with low yield there could be only twenty-thirty cones on hectare of forest massive. Evidently, the measure of aggregation of carpobionts of this breed would be determined not only by their population density, but by the number of cones as well. It can be seen (table 1), that the increasing of cone quantity in crowns attends the decreasing of density levels of three main pests, though in the limits of some plots with different age-structure and forest type the essential

variations in the numbers of cones and the degrees of their settling were observed as being compared to cited means. While the cones develop, the density and aggregation decrease due to mortality of portion of larvae. The values of indices calculated show that they can lead us to different evaluations of SD even for the same sample-series [=excerpts], compared with the threshold values mentioned above. For example, the caterpillars of Laspeyresia strobilella L. (table 1, sample 12) has value A_1 = 3,3, which demonstrates the aggregated type of SD, while the estimation of A_2 = 3.5 - only low crowding level. This is especially true for the samples 9, 10 and 11 in the same table, and, also for the 15th sample pertinent to Lasiomma anthracina Czerny.

Evidently, the discrepancies of SD-estimations are caused just by the origin of the indices: they possess a different apprehensibility and, obviously, are diverse quantitative parameters, characterizing one qualitatively averaged sing - i.e. crowding. Their values estimated for three insect species in cones of firs demonstrate all the spectrum of changings of the SD from random to aggregative. This corroborates the opinion about non-strictness of just the notion "aggregation" (Taylor e.a., 1979). Furthermore, it can be also seen from table 2, that the gregarity in either degree is peculiar to the majority of sample series. This fact also confirms the conclusion (Taylor, 1984) about the dominancy of aggregated type of SD in nature.

During the vegetational period the character of SD changes, though these variations can be uncertain. The decreasing of aggregation-level while the mortality factors operate can be seen from the examples of the four sequential excerpts (No. 1-4 and 5-8 in table 2). In the other plantation (samples No. 9, 10 and 11) the inversed tendency was observed, in spite of expectation of the decreasing of aggregation-degree. Evidently, the uncertainties in the changings of SD-character are caused by the opportunity of different ratios between the number of non-settled cones (which increases as far as the part of pest population is dying off) and the maximal quantity of the larvae in cone (which can be constant due to the optimal microlocal conditions). The last sign determines the length of distributional "tail", and, thus - dispersion values. As a result, the ratios between the density, dispersion and the abundance of non-settled cones, those with only one individual, etc., in different plots of forest massive can be unequal. Hence, the ratios between the estimations pf A_1, A_2 and A_3 can also be uncertain. This shows that we must be cautious during evaluation of SD-character by means of these indices, and generalized conclusion can be made only on the basis of the set of their values.

So far as SD of conobionts is aggregated to one or another level, it is appropriate to analyze it's influence on density estimations when different ways of sampling are applied. It is evident, that any method of sampling is possible when SD is random, and the degree of the errors obtained depends mostly on the quantity of samples taken. When the SD is aggregate, the necessary numbers of samples to obtain the given precise level increases (Odum, 1983). And what is more, the aggregated SD violates non-biased density estimations: the presence of one or more insects in one cone increases the probability of settling the second one, neighbouring with the first. The

Table 1. The comparison of fruiting level of European fir with the degree of settling of cones by insect larvae for Leningrad Distr.

Amount of fruiting	Average number of cones per tree with the diameter of 18-22 sm	Initial population density (numb. per cone) for the larvae		
		Laspeyresia strobilella L.	Lasiomma anthracina Karl.	Kaltenbachiola strobi Winn.
0	1	95 - 100	2 - 6	18 - 50
1	2 - 4	30 - 60	2 - 4	10 - 28
2	20 - 27	26 - 32	1,5 - 3,0	3 - 22
2	60 - 72	12 - 22	0,5 - 1,5	12 - 22
4	120 - 144	1 - 2	0,2 - 0,8	2 - 4
5	180 - 216	0,5 - 1,7	0,1 - 0,8	1 - 6

Table 2. The evaluations of character of SD of fir-tree and pine carpobionts by means of the indices of gomogeneity (for the years with different fruiting). (See notations in text).

N of an excerpt	Date of observation	Amount of fruiting	Size of an excerpt (cones numb.)	Statistical parameters					Estimations of indices		
				$\bar{x}$	σ^2	n_0	n_1	n_2	A_1	A_2	A_3
			Laspeyresia strobilella L.								
1	3.06	2	16	63,7	322,0	0	0	0	5,1	67,7	-
2	12.06	2	14	28,4	87,3	0	0	0	3,1	30,5	-
3	25.06	2	32	7,2	20,3	2	2	1	2,8	9,0	1,0
4	25.08	2	10	1,2	1,0	2	5	2	0,8	1,0	0,3
5	16.06	3	11	13,2	89,7	0	0	0	6,8	19,0	-
6	3.07	3	19	5,0	9,1	0	1	1	1,8	5,9	0
7	10.09	3	10	3,7	6,3	1	1	2	1,7	4,4	4,4
8	25.10	3	20	2,0	2,5	4	3	4	1,3	2,3	3,6
9	15.06	3	27	0,7	0,5	12	11	4	0,7	0,5	0,8
10	3.07	3	27	0,5	0,5	17	7	3	1,0	0,2	2,1
11	9.08	3	37	0,6	0,9	25	5	5	1,5	1,1	10,0
12	1970	4	60	1,2	3,9	33	13	3	3,3	3,5	1,2
			Pegohylemyia antracina Cerny								
13	1968	0	9	2,7	3,4	1	2	1	1,3	3,0	0,5
14	1969	3	7	1,8	1,8	1	2	1	1,0	1,8	0,5
15	1967	5	16	1,4	3,8	6	7	0	2,8	3,2	0
			Kaltenbachiola strobi Winn.								
16	1966	2	18	19,0	36,6	0	0	0	3,2	17,7	-
17	1969	3	195	15,5	49,3	21	0	0	1,9	19,9	-
18	1970	4	60	3,7	37,4	22	8	7	10,1	12,8	4,8

procedure of randomization is recommended (e.g. Jessen, 1978) for the removal of inhomogeneousness of the initial statistical data. But the effectiveness of strict randomization applicable to the exactness of density evaluations was not studied neither for carpobionts nor for many other insects.

The influence of sampling method on the exactness of density estimations was studied, the larvae of Kaltenbachiola strobi Winn. being the example of non-random SD. The number of cones examined (sample size) was large enough to consider that excerpt representative for experiments (195 cones, see sample 17 in the table 2). Four methods of sampling were tested, namely:

- the sequential sampling of neighbouring cones, e.g., No 1-10 or 180-190;

- the systematic non-random access with equal intervals between samples, e.g. 15-th, 25-th, 35-th etc. cones;

- the optionally-random sampling;

- the strictly-random sampling, the numbers of cones being determined by means of list (generator) or random counts.

Five subsamples with equal size of 10 and 20 cones were examined in each variant, the results being reflected in table 3. The data adduced show that the maximal variations of the means obtained in any case is peculiar to 10-th cones subsamples, and between the variants-to the method of sequential sampling of the neighbouring cones. Evidently, the probability of obtaining the precise sample from an infinite set increases from the sequential to the randomized method of sampling. At the same time, strictly organized randomization, which requires a lot of time and labour, rather negligibly increases the accuracy of density evaluations in comparison with the optional or the systematic sampling. Analogical experiments with the larvae other insects species, e.g. clover seed-pests and Leptinotarsa decemlineata Say (unpublished data) allow to formulate such a statistical rule: the influence of randomization procedure on the precision of the means obtained decreases with the increasing of excerpt's size. Though the randomization removes the subjectivity in accessing of a sample, for the endophytious insect it has little significance in this aspect, and, when the fruiting level is low, it is hardly acceptable at all. But the necessity of applying the elements of randomization, particularly for the small excerpts, is evident. This must be taken into account during practical surveying of the programs of sequential sampling. There were also detected, that not only the means calculated but the dispersion as well varies considerably for the same levels of average density when the sequential sampling of neighbouring cones adduced. Hence, the recommended numbers of samples (e.g. Christensen, 1977) would vary considerably. Hitherto, the obtaining at one of the small excerpt for determining the quality of samples require for 10%-th or 15%-th precise level is inexpediently, and more exact is to calculate the values of "a" and "b" constants in Taylor's power law on the basis of many years materials for a priori determining of the usually required excerpt's size (when the program of sequential sampling is not developed). The previous investigations (Stadnitzky, Smetanin, 1985) consider obtaining all the cones from optionally

Table 3. The results of testing of different methods of sampling applicable to the larvae of Kaltenbachiola strobi Winn.: Leningrad Distr., Siversky forest-massive, 1968, 195 cones, mean density $\bar{x}$ = 15,5 individ. per cone.

Method of subsampling	Size of a subsample	Estimations of the means			
		$\bar{x}_{min}$	$\bar{x}_{max}$	$\bar{x}$	for subsamples
Sequential sampling of neighbouring cones	10	7,5	19,5	13,7	
	20	7,9	18,8	15,9	
Systematic non-random access with equal intervals	10	11,8	19,1	16,8	
	20	14,7	18,3	16,8	
Optionally-random sampling	10	15,0	19,6	17,3	
	20	13,8	18,5	16,3	
Strictly-random sampling	10	12,0	18,3	15,3	
	20	13,6	16,5	15,3	

choiced 8-21 trees for the ensuring of 20% precise estimation of the insect population density.

REFERENCES

Christensen, J.B., A.P. Guttierrez, W.R. Cothran and G.G. Summers, 1977: The within field spatial pattern of the larval Egyptian alfalfa weevil, Hypera brunneipennis (Col.: Curculionidae): an application of parameter estimates in simulation. Canad. Entomol. vol. 109, N 12, p. 1599-1604.

Harcourt, D.G., 1963: Population dynamics of Leptinotarsa decemlineata (Say) in Eastern Ontario. I. Spatial pattern and transformation of field counts. Canad. Entomol. vol. 95, N 8, p. 813-820.

Harcourt, D.G., 1965: Spatial pattern of the cabbage looper, Trichoplusia ni, on crucifers. Ann. Entomol. Soc. Amer. vol. 58, N 1, p. 89-94.

Jessen, R.J., 1978: Statistical survey techniques. John Wiley & Sons, N.Y. - Toronto, 478 p.

Mirkin, B.M. and G.S. Rosenberg, 1983: Explanatory dictionary of modern Phytocoenologie. Moscou, 133 p.

Odum, E., 1983: Basis ecology. Vol. 2. Saunders Coll. Publ., 376 p.

Stadnitzky, G.V. and A.M. Bortnik: 1976: Statial theory of insect population dynamics. Annu. Readings in the mem. of N.A. Cholodkovsky. Leningrad, 1977, p. 44-65.

Stadnitzky, G.V. and G.M. Smetanin, 1985: On the calculation and prediction of the yields of softwoods seeds. Journal of Forestry, N 1, pp. 22-27.

Taylor, L.R., J.P. Woiwud and J.N. Perry, 1979: The negative binomial as a dynamic biological model for aggregation and the density dependence of K. Journal of Animal Ecology, vol. 48, N 1, pp. 283-304.

Taylor, L.R., 1984: Assessing and interpreting the spatial distribution of insect populations. Ann. Rev. Entomol., vol. 29, Palo Alto (Caliph), pp. 321-357.

RESPONSES OF DIORYCTRIA CLARIORALIS, D. DISCLUSA, AND D. MERKELI TO PHEROMONE BAITS IN GEORGIA AND TEXAS

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SUMMARY

Pheromones have been identified for four sympatric species of Dioryctria, D. amatella (Hulst), D. disclusa (Heinrich), D. clarioralis (Walker), and D. merkeli (Mutura and Munroe), which are important pests in pine seed orchards in the southeastern United States. A study was conducted to confirm the relative attractiveness and inhibition of 100 µg Z9-14:Ac and 88 µg Z9-14:Ac + 12 µg E9-14:Ac + 10 µg Z11-16:Ac for each of these species throughout their flight periods in Georgia and Texas. The single-component bait attracted more D. merkeli than did the three-component bait, while the three-component bait attracted more D. clarioralis than did the single-component bait. D. disclusa was equally attracted to both baits. No regional differences in male response to the pheromone baits were observed, but numbers of D. clarioralis captured varied greatly with season. The significance of these observations relative to species isolation mechanisms and operational Dioryctria surveys are discussed.

INTRODUCTION

Coneworms (Dioryctria spp., Lepidoptera: Pyralidae) are among the most important insects limiting production of highly valuable seeds in pine seed orchards across the southeastern United States (Ebel et al. 1975; Fatzinger et al. 1980). Sympatric coneworm species common to this region include, D. amatella (Hulst) (DA), D. clarioralis (Walker) (DC), D. disclusa (Heinrich) (DD), and D. merkeli Mutura and Munroe (DM). Female sex pheromone components identified for these Dioryctria spp. include (Z)-11-hexadecenyl acetate (Z11-16:Ac) for DA, (Z)-9-tetradecenyl acetate (Z9-14:Ac) for DD, and Z9-14:Ac + 12% (E)-9-tetradecenyl acetate (E9-14:Ac) for DC (Meyer et al. 1982; Meyer et al. 1984; Meyer et al. 1986). The addition of 5-10% Z11-16:Ac greatly enhanced the attraction of DC males to Z9-14:Ac + 12% E9-14:Ac (Meyer et al. 1984). Males of DM also are attracted to Z9-14:Ac and Z9-14:Ac + E9-14:Ac (Cameron 1981; Hanula et al. 1984; Meyer et al. 1984).

Synthetic sex pheromones are being used to detect the presence and relative numbers of Dioryctria moths in pine seed orchards throughout the Southeastern United States (DeBarr et al. 1981; DeBarr and Berisford 1984; Weatherby et al. 1985). Two pheromone single-component baits (Z9-14:Ac) in separate sets of traps have been used because of strong inhibition of DD and DM by the DA pheromone (Z11-16:Ac) and the cross attraction of DC and DM to the DD pheromone (Z9-14:Ac) (Hanula et al. 1984).

However, certain questions generated by previous field studies indicate a need for further research on the pheromones of Dioryctria species in the South. The addition of 3.6 µg E9-14:Ac to 30 µg Z9-14:Ac significantly increased the numbers of DC males captured in a field test conducted in Texas (TX) and the addition of 5-10% Z11-16:Ac enhanced the attractiveness of this two-component bait even more in another Texas field test (Meyer et al. 1984). But in a test conducted in Georgia (GA), the addition of 3.6 µg E9-14:Ac to 30 µg Z9-14:Ac significantly reduced the numbers of DC males captured and the addition of 300 µg Z11-16:Ac had no apparent effect on the numbers of DC males captured (Hanula et al. 1984). These results suggest the possibility of regional differences in response of DC to synthetic pheromones. Intraspecific geographical variation in male response has been documented for several groups of Lepidoptera (Cardé and Baker 1984), and temporal changes in male moth response also may occur (Bogenschutz 1980).

DC has three distinct generations per year (Ebel et al. 1975) and three resulting flight periods throughout the southeastern United States as demonstrated in numerous light-trap studies (Merkel and Fatzinger 1971; Yates and Ebel 1975; Cameron 1981; Tauer et al. 1983). In earlier pheromone studies conducted in Texas, there appeared to be seasonal variation in the effectiveness of the DC baits tested. High numbers of males were caught during the spring while low numbers were caught during subsequent flight periods, even though many male moths were captured in black-light traps during these periods (Meyer et al. 1984). Low numbers of DC males have been observed repeatedly during the summer generation in pheromone traps baited with 100 µg Z9-14:Ac (Weatherby et al. 1985, USDA Forest Service, unpublished data).

None of the previous studies was intended to distinguish geographical or seasonal differences in response to different pheromone blends. The study reported here was specifically designed to compare the relative attractiveness of the standard single-component "DD bait" (100 µg Z9-14:Ac) currently used to trap male DC, DD, and DM moths in seed orchards (Weatherby et al. 1985) with that of the three-component "DC bait" (88 µg Z9-14:Ac + 12 µg E9-14:Ac + 10 µg Z11-16:Ac) throughout the flight periods of these three Dioryctria species in two widely separated geographical regions.

METHODS

Field tests of the "DD bait" and the "DC bait" were conducted from April through October, 1985, in two unprotected loblolly pine (Pinus taeda L.) seed orchards, one located in Jasper County, TX and the other in Putnam County, GA. In both study orchards, Pherocon® 1C traps (Zoecon Corp.) were positioned in the tops of 20 of the tallest trees spaced at least 10 m apart

in a large circle. Ten replicates of each treatment were located alternately around the circle starting on 2 April 1985, in Texas, and 16 April 1985, in Georgia. Dioryctria moths were removed, identified, and sexed, and traps were rotated to the next position at ca. weekly intervals until 12 November in Texas and 19 October in Georgia. Fresh baits were placed in traps every four weeks and sticky trap bottoms were changed as often as needed to maintain their effectiveness. Differences in numbers of moths caught between treatments at each site were tested for significance with a paired "t"-test using total weekly trap catches as replicates.

A 110 volt AC-powered 50 cm black-light trap described by Cameron (1981) was operated two nights per week from 10 March through 4 November during 1985. This trap was located in a small stand of mature loblolly and shortleaf (P. echinata Mill.) pine trees ca. 300 m from the pheromone trapping study area. Insects were collected in a 1 liter jar partially filled with isopropyl alcohol and Dioryctria spp. were sorted by species and sexed.

RESULTS AND DISCUSSION

The numbers of DC, DD, and DM male moths caught on pheromone traps at the Georgia and Texas sites are presented in Table 1. DC strongly preferred the three component "DC bait" over the single component "DD bait" (ca. 6.5:1) at both study sites, while the reverse was true for DM, which preferred the "DD bait" (ca. 7.7:1) (Table 1). Thus, we conclude that there are no apparent regional differences for these two species in pheromone responses to the two baits tested, based upon populations observed in Georgia and Texas.

In Texas only one DD moth was caught on the "DC bait," while relatively large numbers of DD moths were captured in Georgia on both the one-component "DD bait" and the three-component "DC bait." Although the "DD bait" caught about 20% more DD moths than the "DC bait," there was no significant difference between treatments. This conflicts with the results of a previous test conducted in Georgia which showed that DD males were strongly inhibited by the addition of E9-14:Ac and/or Z11-16:Ac (Hanula et al. 1984).

The numbers of DC moths captured in pheromone traps in Georgia and Texas and in the light trap in Texas during each of three flight periods are presented in Table 2. The initiation of the first flight period may have been missed in Georgia and Texas since moths were caught in both locations during the first week of trapping. Each flight period appeared to be similar in time of occurrence and duration in Georgia and Texas. Reduced numbers of male moths were captured in pheromone traps in Georgia and in the light trap in Texas during the mid-summer generation, but no DC males were captured in pheromone traps in Texas during this period. A total of 37 DC moths were captured in the Texas light trap during the summer flight period indicating that DC moths were in the general area of the pheromone trapping study site, but the majority were females (Table 2). The ratios of males:females were substantially higher among light trap catches during the spring and fall flight periods.

Table 1. Numbers of Dioryctria clarioralis (DC), D. disclusa (DD) and D. merkeli male moths caught in pheromone traps in loblolly pine seed orchards in Jasper County, TX, and Putnam County, GA during 1985.

Coneworm species	Location	Total males captured* DC bait	DD bait	t-test PR>/T/
D. clarioralis	GA	282	46	0.01
	TX	266	36	0.02
D. disclusa	GA	1012	1218	0.12
	TX	1	0	-
D. merkeli	GA	35	283	0.03
	TX	27	181	0.01

* DC bait = 88 µg Z9-14:Ac + 12 µg E9-14:Ac + 10 µg Z11-16:Ac;
DD bait = 100 µg Z9-14:Ac.

Table 2. Numbers of Dioryctria clarioralis male moths captured by flight period in pheromone traps in Jasper County, TX and Putnam County, GA and in a light trap (LT) in Texas during 1985.

Flight period	Location	Julian dates	Total males captured* DC bait	DD bait	Moths caught in LT Male	Female	ratio M:F
1	GA	106-127	73	4	-	-	-
	TX	92-126	127	16	36	24	1.5
2	GA	168-240	29	9	-	-	-
	TX	161-240	0	0	10	27	0.4
3	GA	241-297	180	33	-	-	-
	TX	241-295	139	20	34	41	0.8

* DC bait = 88 µg Z9-14:Ac + 12 µg E9-14:Ac + 10 µg Z11-16:Ac;
DD bait = 100 µg Z9-14:Ac.

Drastically changing sex ratios among flight periods also were observed in a light trap study conducted at this orchard site in 1981 (Cameron and Riggs, unpublished report[1]). If DC moths were present in the same male:female ratios in the pheromone trapping area as around the light trap during mid-summer, the heavy competition among natural females for the few males in the area might partially account for the absence of DC males in the pheromone traps during mid-summer. Other possible reasons for a lack of male DC moths in pheromone traps include: 1) a reduction in numbers of DC moths present in the seed orchard during this season, possibly due to aestivation of a portion of the population, 2) a seasonal decline in male pheromone response, 3) changes in pheromone emission rate or dispersal pattern related to weather conditions and/or 4) other unrecognized factors.

Reproductive isolation mechanisms for the sympatric coneworm species common in southern pine seed orchards have been discussed by several authors (Cameron 1981; Hanula et al. 1984; Meyer et al. 1984), and involve chemical, seasonal, and diel components. However, the role of pheromones in isolating DM from DC moths during their overlapping late summer flight periods has not been previously recognized. Hanula et al. (1984) demonstrated that DM was strongly inhibited by the addition of large amounts (300 µg) of Z11-16:Ac to baits containing 30 µg Z9-14:Ac and 30 µg Z9-14:Ac + 3.6 µg E9-14:Ac. In our study the small amounts of Z11-16:Ac contained in the three-component DC bait (similar to the very small quantities apparently produced by DC females), also strongly inhibited the response of DM male moths. Thus, it appears that differences in diel activity patterns (Cameron 1981) and pheromone communication are key factors in the reproductive isolation of DC and DM moths.

Results of our study have important implications for how pheromones are used for survey and control. The three-component DC bait would be preferrable to the less attractive single-component DD bait for DC mating disruption operations. But the DD bait may be adequate for survey purposes. Assuming that the numbers of DC males captured in DD baited traps are consistently correlated to actual populations, the "weaker" DD bait may even be preferred in order to avoid trap saturation (Bogenschutz 1980; Daterman 1980). However, neither bait appears to be reliable for monitoring DC during mid-summer. This may not hinder surveys in loblolly pine seed orchards since DC damage apparently is rare in loblolly pine seed orchards in Georgia and surrounding states (DeBarr, personal communication) and significant DC damage has only been observed following the spring flight period in Texas orchards (Cameron 1981).

The results of this and previous studies reveal considerable variability associated with the pheromone communication systems utilized by species of Dioryctria. The complexities of these pheromone systems suggest that further research is warranted.

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[1] Cameron R. S. and C. D. Riggs. 1983. Coneworm moths (Dioryctria spp.) captured in black light traps at the Magnolia Springs Seed Orchard near Kirbyville, TX, during 1981 and 1982. Tex. For. Serv. Report No. 83-5. 12 pp.

LITERATURE CITED

Bogenschutz, H. 1980. Survey of pine defoliators in central Europe using sex attractants. pp. 51-65. In A. A. Berryman and L. Safranyik (eds). Proc. Second IUFRO Conf. Dispersal of Forest Insects: Evaluation, Theory and Management Implications. Sandpoint, ID. 27-31 August 1979.

Cameron, R. S. 1981. Toward insect pest management in southern pine seed orchards with emphasis on the biology of Tetyra bipunctata (Hem., Pentatomidae) and the pheromone of Dioryctria clarioralis (Lep., Pyralidae). Texas For. Serv. Publ. 126. 149 pp.

Cardé, R. C. and T. C. Baker 1984. Sexual communication with pheromones. pp. 355-383. In W. J. Bell and R. T. Cardé (eds). Chemical Ecology of Insects. Sinauer Associates, Inc. Sunderland, MA.

Daterman, G. E. 1980. Pheromone responses of forest Lepidoptera: implications for dispersal and pest management. pp. 251-265. In A. A. Berryman and L. Safranyik (eds). Proc. Second IUFRO Conf. on Dispersal of Forest Insects: Evaluation, Theory and Management Implications. Sandpoint, ID. 27-31 August 1979.

DeBarr, G. L., and C. W. Berisford. 1984. Use of sex pheromones for seed and cone insect pest management in conifer seed orchards. pp. 194-203. In H. O. Yates, III (ed.), Proc. Cone and Seed Insects Working Party Conference, Athens, GA. IUFRO, Southeastern For. Exp. Sta. Athens, GA. 31 July - 6 August 1983.

DeBarr, G. L., L. R. Barber, C. W. Berisford, and J. C. Weatherby. 1981. Pheromone traps detect webbing coneworms in loblolly pine seed orchards. So. J. Appl. For. 6: 122-127.

Ebel, B. H., T. H. Flavell, L. E. Drake, H. O. Yates, III, and G. L. DeBarr. 1975. Seed and cone insects of southern pines. USDA For. Serv. Gen. Tech. Rep. SE-8. 40 pp.

Fatzinger, C. W., G. D. Hertel, E. P. Merkel, W. D. Pepper, and R. S. Cameron. 1980. Identification and sequential occurrence of mortality factors affecting seed yields of southern pine seed orchards. USDA For. Serv. Southeastern For. Exp. Sta. Res. Pap. No. SE-216. 43 pp.

Hanula, J. L., C. W. Berisford, and G. L. DeBarr. 1984. Pheromone cross-attraction and inhibition among four coneworms, Dioryctria spp. (Lepidoptera: Pyralidae) in a loblolly pine seed orchard. Environ. Entomol. 13: 1298-1301.

Merkel, E. P., and C. W. Fatzinger. 1971. Periodic abundance of pine cone-infesting Lepidoptera in black light traps and sleeve cages in north Florida. Florida Entomol. 54: 53-61.

Meyer, W. L., G. L. DeBarr, C. W. Berisford, L. R. Barber, and W. L. Roelofs. 1982. Identification of the sex pheromone of the webbing coneworm moth, Dioryctria disclusa (Lepidoptera: Pyralidae). Environ. Entomol. 11: 986-988.

Meyer, W. L., R. S. Cameron, A. Tamhankar, G. DeBarr, C. W. Berisford, and W. L. Roelofs. 1984. Sex pheromone of the blister coneworm moth, Dioryctria clarioralis (Lepidoptera: Pyralidae). Environ. Entomol. 13: 854-858.

Meyer, W. L., G. L. DeBarr, J. L. Hanula, B. Kovalev, R. S. Cameron, C. W. Berisford, and W. L. Roelofs. 1986. Z-11 hexadacenyl acetate, a sex pheromone for the southern pine coneworm, Dioryctria amatella (Lepidoptera: Pyralidae). Environ. Entomol. 15: 316-320.

Tauer, C. G., R. D. Eikenbary, and G. M. LeHar. 1983. Light trapping cone and seed insects (Lepidoptera: Tortricidae and Pyralidae) of pine in southeastern Oklahoma. Environ. Entomol. 12: 753-757.

Weatherby, J. C., G. L. DeBarr, and L. R. Barber. 1985. Monitoring coneworms with pheromone traps: a valuable pest detection procedure for use in southern pine seed orchards. pp. 208-220. In Proc. of the Eighteenth Southern Forest Tree Improvement Conference, Long Beach, MS.

Yates, H. O., III, and B. H. Ebel. 1975. Light trapping and identifying Dioryctria that damage pine cones in northeastern Georgia (Lepidoptera: Phycitidae). J. Georgia Entomol. Soc. 10: 78-86.

SPATIAL DISTRIBUTION OF TAMARACK CONES AND THOSE INFESTED BY A CONE MAGGOT, *STROBILOMYIA* SP. (DIPTERA: ANTHOMYIIDAE), IN ONTARIO: PRELIMINARY RESULTS

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ABSTRACT

The number of cones produced by 3-8m tall tamaracks, *Larix laricina* (Du Roi) K. Koch, was highest in the mid-crown and the southern quadrant. However, the vertical distribution of cones varied with the number of cones per tree; the proportion of cones located in the upper third of the crown increased as the number of cones per tree increased, a relationship not observed at the other crown levels. The relationship between tree height and the number of cones per tree was positive and linear ($p < 0.05$). Both the number and the proportion of cones infested by a cone maggot, *Strobilomyia* sp., were significantly higher in the upper and mid-crown than in the lower crown. The vertical distribution of infested cones was also influenced by the number of cones per tree. The number, but not the proportion, of damaged cones was affected by the cardinal direction. Variation in the number of cones attacked per tree can be explained partly by tree height; taller trees bore more infested cones than shorter trees.

RESUME

Le tiers median, et le quadrant sud du tamarac, *Larix laricina* (Du Roi) K. Koch, (3-8m de hauteur) furent les plus fournis en cônes. La stratification des cônes fut influencée par le nombre de cônes présent sur l'arbre: la proportion de cônes situés dans le tiers supérieur augmenta avec la production de cônes de l'arbre, une relation n'existant pas dans les tiers médian et inférieur. La relation entre la taille des arbres et le nombre de cónes par arbre fut linéaire et positive. Le nombre et la proportion des cônes attaqués par la mouche des cônes, *Strobilomyia* sp, furent significativement plus élevés dans les strates supérieure et médianne qu'inférieure. La stratification des cônes attaqués fut également influencé par le niveau de production de l'arbre. Les différences constatées dans le nombre de cônes attaqués par quadrant furent significatives et correspondaient aux différences de production dans ces mêmes quadrants. Le nombre de cônes attaqués par *Strobilomyia* sp. fut plus élevé chez les arbres les plus grands.

INTRODUCTION

In Canada, breeding programs to improve larches, especially tamarack, Larix laricina (Du Roi) K. Koch, were initiated recently (Simpson 1983, Rauter & Graham 1983). More than 20 ha of seed orchards have already been established (Pollard 1981) to ensure the regular production of high quality seeds needed for reforestation. Insects infesting the reproductive structures of conifers represent, especially in seed orchards, one of the most serious threats to seed viability (Coulson & Witter 1984). Around the world, cone maggots, Strobilomyia sp. gen. n. (= Lasiomma Stein (Diptera: Anthomyiidae), Michelsen 1988) are currently recognized as the most important internal feeders of larches (Amirault 1984, Eavy 1987, Roques et al. 1983, 1984, Stadnitsky et al. 1974). In New Brunswick, the cone crop of tamarack, was significantly reduced by the cone maggot, S. viaria (Huckett), which infested up to 85% of the cones (Amirault & Brown 1986). However, subsequent examination of these specimens, and those of Eavy (1987), revealed that another species, S. laricis sp. n. (= Lasiomma laricicola in North American literature), was equally important in inflicting damage to tamarack cones (Michelsen 1988). Little is known concerning the geographic distribution of these maggots in Canada, but, based on available records, it is suspected that both species are present in Ontario (V. Michelsen, personal communication)[1].

There is scant information on the life history and the bionomics of both S. viaria and S. laricis (Amirault 1984, Michelsen 1988) although they are not expected to differ markedly from those of maggots infesting the cones of spruces in Canada (Tripp & Hedlin 1956, Hedlin 1973, Tripp 1954) or larches in France (Roques et al. 1984) and USSR (Stadnitsky et al. 1974). Cone maggots are univoltine and overwinter as a puparium in the litter (Michelsen 1988), near the tree stem (Fogal 1986). Adult emergence begins early in the spring and may last for several weeks. Oviposition usually occurs at a specific phenological stage of cone development, which varies among species (Roques et al. 1984). There are three larval instars although the first molt occurs within the egg (Tripp 1954). Larvae feed for approximately one month. Extended diapause usually plays an important role in the population dynamics of cone maggots (Roques et al. 1984, Roques in press, Michelsen 1988).

Sampling schemes represent the basis of pest management programs (Ruesink & Kogan 1975). These schemes are needed to accurately evaluate pest densities and to monitor their fluctuations, as well as to assess the pest's impact on yields and the efficacy of management tactics. Knowledge of the spatial distribution of cones and those infested by a pest is not only a requisite to the development of sampling schemes, but is also essential to foresters and entomologists concerned with harvesting and protecting cones. Currently, there is no information on the spatial distribution of any of the pests infesting the cones and seeds of tamarack in Canada. However, the distribution of S. melania Ackl., a pest of the European larch, Larix decidua Mill., in France has

1. I recently initiated a study on the distribution of these two species in Canada. The specimens collected in this study have been sent for identification.

been examined and sampling schemes have been developed (Roques in press). The distribution of cones on young tamarack was recently examined, although emphasis was placed mainly on the type of shoots producing cones and the position of the cones on the shoots (Tosh 1986).

The objective of this study was to identify the distributional pattern of tamarack cones and those infested by Strobilomyia sp.. The results of this work are reported herein.

MATERIALS AND METHODS

The distribution of cones and cones infested with third-instar Strobilomyia sp. was examined by selecting, in June 1987, 12 tamaracks growing openly in two fields, 20 km west of Cochrane, Ontario. Trees were 3 - 8 m tall. The living crown of each tree was divided into 12 cells: three strata (upper, mid and lower) and four quadrants (N, E, S, W) which were established using the NE, SE, SW, and NW compass bearings. The cones from each cell were removed by hand and placed in separate bags. The number of cones and those infested by Strobilomyia sp. were determined for each cell. Whether S. viaria and S. laricis infest cones of the same tree is currently unknown.

To investigate if the position of the cones on the branch had an effect on the number and proportion of infested cones, an additional 14 trees were selected and two whole branches from each crown level were sampled. The number of cones, and those infested, in the proximal and distal half of each branch was determined.

For statistical analyses, counts of cones and infested cones were tranformed to their $\log_e (x+1)$ counterparts, whereas the proportions were transformed by arc sin proportion to stabilize the variances. Unless mentioned otherwise, untransformed means are presented. Analyses of variance (ANOVA), where the effects of tree, strata, quadrant (and cone location on the branch, when applicable) and their interactions were considered simultaneously, were performed using PROC ANOVA (SAS Institute 1985, 113-137). Following a significant ANOVA, means were separated using Duncan's New Multiple Range test. To account for a statistically significant interaction, a subsequent ANOVA and means-comparison test was performed using the interaction as error term.

RESULTS and DISCUSSION

In this study, all Strobilomyia-infested cones contained a single third-instar larva. Although carefully examined, no cadavers were detected, suggesting that at the observed cone density, only one egg was laid per cone. The frequency distribution of eggs per cone is currently being determined. The number of S. melania eggs found on European larch cones varies greatly with cone production levels but may reach 15 (Roques in press). It is possible that for tamarack, cone size is another limiting factor for the number of eggs laid per cone as it appears unlikely that two larvae could fully develop within a single cone.

Among-tree variation. The number of cones, as well as the number and the proportion of Strobilomyia sp. infested cones, varied significantly among trees (ANOVA: $F = 91.49$, 28.38 and 9.51 with $df = 11, 132$, $p < 0.0001$). Part of the variation in the numbers of cones, and cones infested, among trees can be explained by variations in tree height (Fig. 1). In young tamarack, the number of cones per tree is highly correlated to tree height (Tosh 1986).

The relationship between the number of cones infested per tree and the number of cones on the same tree (Regression analysis: $R^2 = 0.33$; $F = 4.83$; $df = 1, 11$; $p = 0.053$) is weak, probably due to one outlier (Fig. 2). However, when this outlier is removed (there is no methodologically identifiable reason to remove this observation except to demonstrate its significance), the percent of the variation in infestation levels explained by the new regression equation, increases from 33% to 68% ($R^2 = 0.68$; $F = 19.8$; $df = 1, 10$; $p = 0.002$), suggesting that the significance of cone abundance in predicting the number of cones infested per tree is probably slightly higher than observed here. For S. melania, two components appeared significant in explaining the distribution of infested cones. In the first component, the number of damaged cones per tree varies in relation to the joint effect of cone crop size and previous damage by another maggot, S. laricicola Karl, whereas the second component corresponds to a stand factor in which tree height and altitude had opposite effects (Roques in press).

There was no evidence of a relationship between the proportion of infested cones per tree and cone density (Regression analysis: $R^2 = 0.08$; $F = 0.89$; $df = 1, 11$; $p > 0.367$) (Fig. 3), indicating that Strobilomyia sp. does not prefer trees with more cones to oviposit.

Within-tree variation. The cardinal direction had a significant effect on the mean number of cones (ANOVA: $F = 22.51$; $df = 3, 140$; $p < 0.0001$), and those infested by Strobilomyia sp. ($F = 13.22$; $df = 3, 140$; $p < 0.0001$) (Table 1). However, the distributional pattern of the Strobilomyia-infested cones and the cones was similar, with the south quadrant supporting the highest densities. Consequently, the proportion of cones infested did not vary significantly ($F = 1.94$; $df = 3, 140$; $p > 0.1318$) indicating that Strobilomyia sp. does not attack any quadrant disproportionately.

There were no significant differences between the number of cones (ANOVA: $F = 0.08$; $df = 1, 166$; $p < 0.7830$), or cones infested by Strobilomyia sp. ($F = 1.02$; $df = 1, 166$; $p < 0.3149$), located in the proximal and distal portions of the branch. After accounting for the significant interaction between cone location and strata ($F = 4.89$; $df = 2, 166$; $p < 0.0095$), differences in the proportion of cones infested in each branch portion were not statistically significant ($F = 1.92$; $df = 1, 3$; $p < 0.3000$). However, because of the interaction, I compared for each stratum the proportion of infested cones in each half of the branch (Fig. 4). The results indicated that in the upper crown, the proportion of cones in the proximal half of the branch was significantly higher than in that of the distal half ($t = 3.4629$; $df = 45.6$; $p < 0.0012$). The reasons for this difference are not clear. The differences observed in the mid and lower crown levels were not statistically significant. The

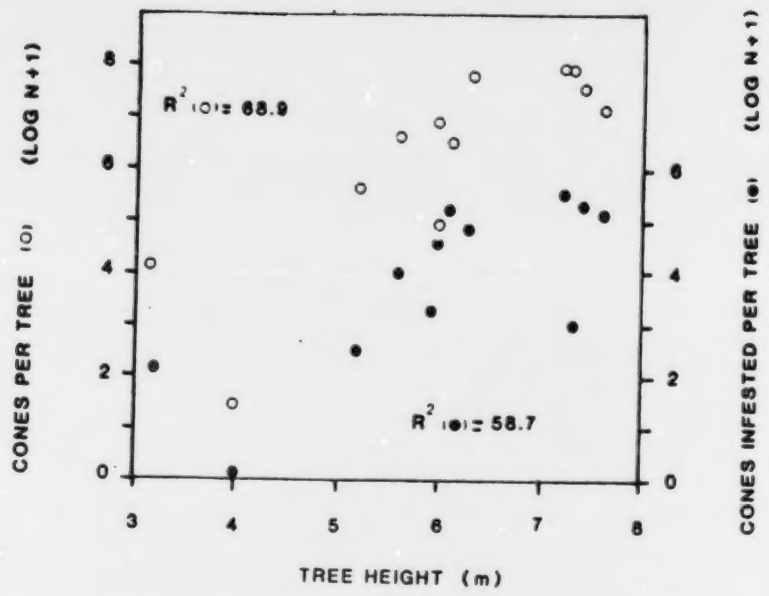

Fig. 1. Number of cones per tree (○) and cones infested by Strobilomyia sp. (●) in relation to tree height near Cochrane, Ontario.

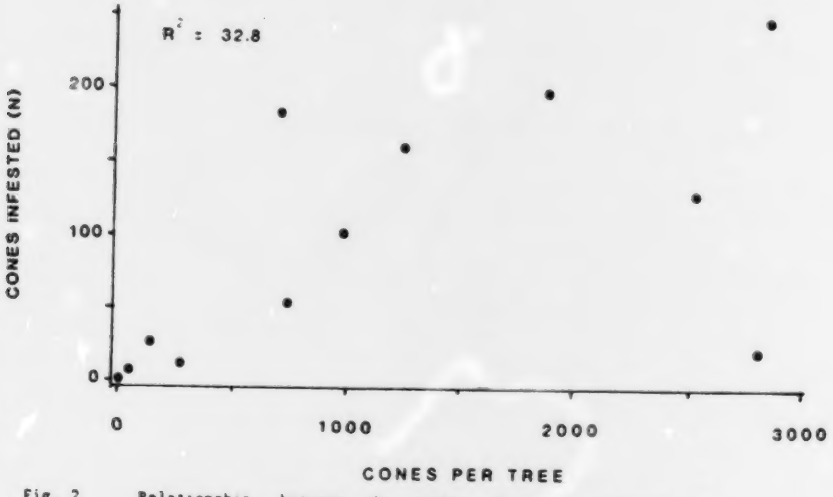

Fig. 2. Relationship between the number of cones infested by Strobilomyia sp. per tree and the number of cones on the same tree.

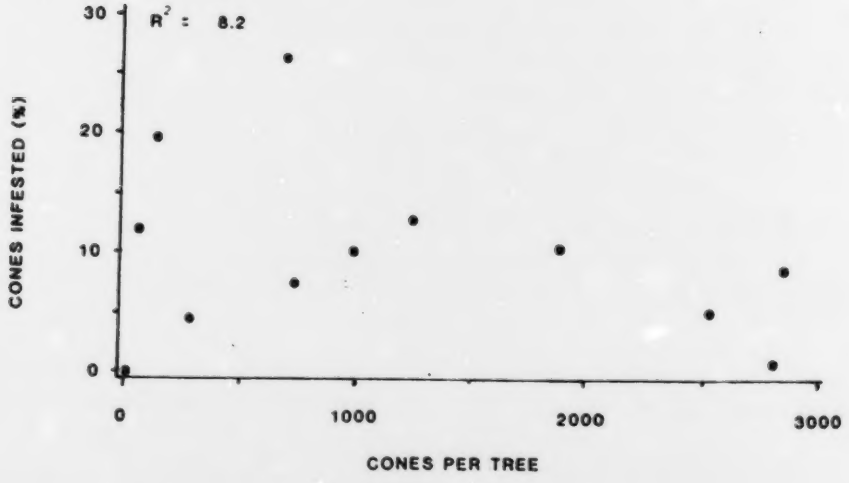

Fig. 3. Proportion of cones per tree infested by Strobilomyia sp. in relation to total number of cones per tree.

Table 1. Mean number of cones, cones infested by Strobilomyia sp. and mean proportion of cones infested in the crown of tamarack.

STRATA	QUADRANT				
	N	E	S	W	Overall Means
Cone Number					
UPPER	54.1	73.0	134.3	75.8	**84.3 b**
MID	118.3	185.5	234.8	127.4	**166.5 a**
LOWER	30.2	38.7	88.0	25.2	**45.5 b**
Overall means	**67.5 bc**	**99.1 b**	**152.4 a**	**76.1 c**	-
Number of Infested Cones					
UPPER	6.7	6.8	16.7	10.3	**10.1 a**
MID	8.6	9.7	17.3	10.9	**11.6 a**
LOWER	1.4	1.4	4.2	0.8	**2.0 b**
Overall means	**5.6 b**	**6.0 b**	**12.7 a**	**7.3 b**	-
Proportion of Infested Cones					
UPPER	11.5	9.6	19.6	14.3	**13.7 a**
MID	9.1	7.1	11.5	9.2	**9.2 a**
LOWER	3.7	6.5	3.6	4.4	**4.6 b**
Overall means	**8.1 a**	**7.7 a**	**11.6 a**	**9.3 a**	-

position of the cones on a branch did not appear to influence the distribution of European larch cones infested by S. melania (Roques in press).

The mean number of cones varied significantly among strata (ANOVA: $F= 18.93$; $df= 2, 24$; $p< 0.0001$) with the mid-crown bearing 3-4 times more cones than the lower crown (Table 1). This distribution of cones corresponded closely to that observed by Tosh (1986). The mean number of cones infested by Strobilomyia sp. larvae also varied between strata ($F= 11.05$; $df= 2, 24$; $p< 0.0005$). Approximately five times more cones from the mid and upper crown were more infested than from the lower crown. The proportion of cones from the upper and the mid strata that were infested by Strobilomyia sp. was similar but significantly higher than the lower crown ($F= 7.05$; $df= 2, 24$; $p< 0.0043$). These statistically significant differences were obtained after accounting for a significant interaction between tree and strata for the number of cones ($F= 3.34$; $df= 22, 143$; $p< 0.0001$), the number of cones infested ($F= 4.43$; $df= 22, 143$; $p< 0.0001$) and the proportion of cones infested ($F= 1.73$; $df= 22, 143$; $p< 0.0001$).

This interaction indicated that the vertical distribution of both the cones, and those infested were influenced by the number of cones per tree. Indeed, the proportion of cones located in the upper crown of trees increased significantly with cone density (Regression analysis: $R^2= .38$; $F= 6.12$; $df= 1, 11$; $p< 0.033$) (Fig. 5). No statistically significant trends were observed in the mid and lower crown levels. The vertical distribution of Strobilomyia-infested cones on attacked trees was similar to the distributional pattern of cones, but only at low cone density (Fig. 5), as the increase in the proportion of infested cones from the tree that was located in the upper crown ($R^2= .67$; $F= 18.12$; $df= 1, 10$; $p< 0.002$) exceeded by far the increase in the proportion of cones produced in that stratum. The decrease in the proportion of Strobilomyia-infested cones from the mid and lower crown levels was significant ($R^2= .39$; $F= 5.84$; $df= 1,10$; $p< 0.039$ for both crown levels).

Because the distributional patterns of the proportion of cones and infested cones change with the tree's cone density and because the study was conducted in only one stand (Miller (1986) reported that the distributional pattern of the Douglas-fir cone gall midge varied among orchards with different levels of cone production), it is difficult at this stage, to determine and recommend which crown level(s) should be sampled to assess infestation levels. On European larch, the distributional pattern of S. melania-infested cones was similar to that of the cone whatever the cone density (Roques in press). As a result, damage by S. melania could be assessed from any crown level as long as it was referred to the cone production of that level (Roques in press). A similarity between the distribution of cones and those infested was also observed for several insects infesting the cones of red pine (Mattson 1976), slash pine (DeBarr et al. 1975), and jack pine (Rauf & Benjamin 1983).

Information on the distribution of viable seeds within tree crowns as well as knowledge of the behavior and of the mechanisms involved in

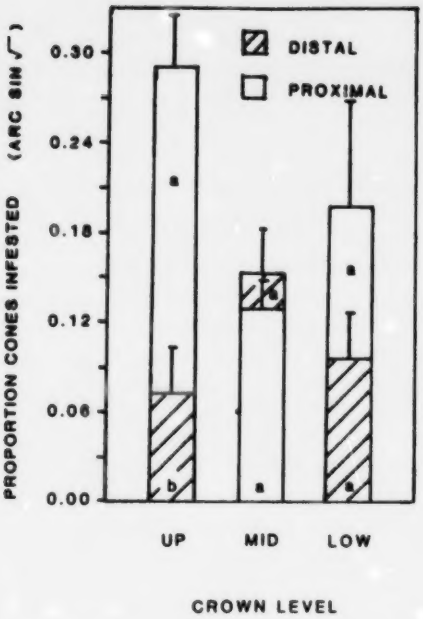

Fig. 4. Comparison between the proportion of cones (transformed) infested by Strobilomyia sp. in the distal and proximal section of branches collected from the upper, mid and lower strata of 3-8 m tall tamaracks.

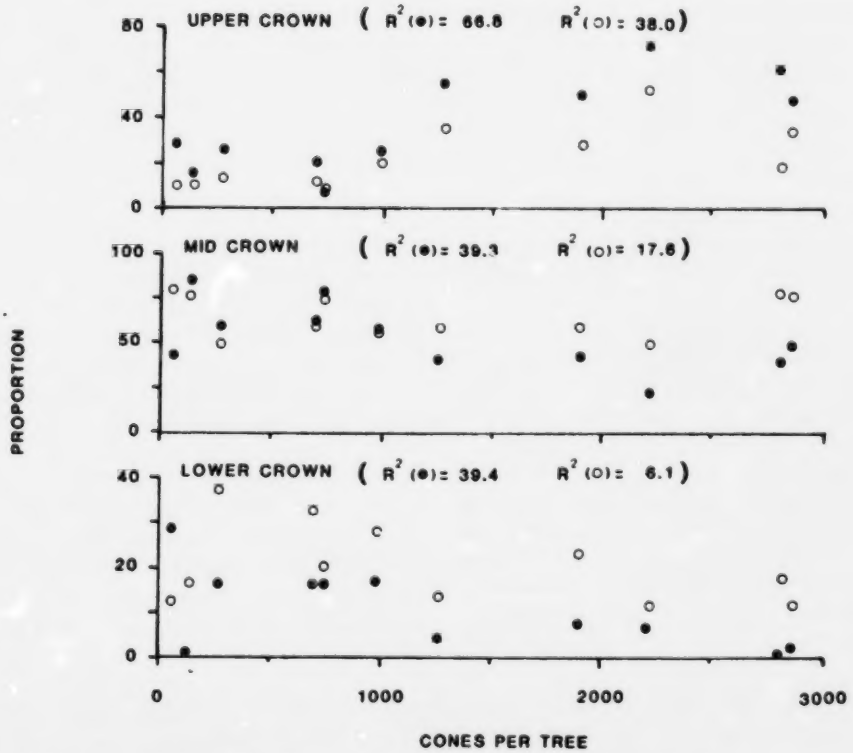

Fig. 5. Relationship between the proportion of cones (○) and Strobilomyia-infested cones (●) located in each of the three crown levels of attacked trees and the number of cones per tree.

the location and selection of cones for oviposition, may provide a better understanding of the results obtained.

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REFERENCES

Amirault, P.A. 1984. An investigation of the cone and seed insects of eastern larch, Larix laricina (Du Roi) K. Koch, and attempts to control damage using chemical insecticides. M.Sc.F. dissertation, University of New Brunswick.

Amirault, P.A. & N.R. Brown. 1986. Cone and seed insects of tamarack, Larix laricina (Du Roi) K. Koch, and attempts to control damage with chemical insecticides. Can. Entomol. 118: 589-596.

Coulson, R.N. & J.A. Witter. 1984. Forest Entomology - Ecology and Management. Wiley Interscience publication, N.Y.

DeBarr, G.L., L.R. Barber & R.C. Wilkinson. 1975. Within-crown distribution of cone and seed insect damage to slash pine flowers, conelets and cones. Florida Entomol. 58: 281-288.

Eavy, A.L. 1987. Cone and seed mortality factor distribution in two natural populations of tamarack in central Maine. Ph.D. dissertation, University of Maine.

Fogal, W.H. 1986. Applying Beauvaria bassiana to soil for control of the spruce cone maggot, Lasiomma anthracina (Czerny). pp. 257-266, IN: Roques, A. (comp. & ed.) Proceedings of the 2nd conference of the cone and seed insects working party (IUFRO) S2.07-01, Briancon, France.

Hedlin, A.F. 1973. Spruce cone insects in British Columbia and their control. Can. Entomol. 105: 113-122.

Hedlin, A.F., H.O. Yates III, D. Cibrian Tovar, B.H. Ebel, T.W. Koerber & E.P. Merkel. 1980. Cone and seed insects of North American conifers. Canadian Forestry Service / USDA forest Service / Secretaria de Agricultura y Recoursos Hidraulicos, Mexico.

Mattson, W.J. 1976. Distribution of the cone insect, Dioryctria disclusa, in red pine trees. USDA Forest Service, Res. Paper NC-136.

Michelsen, V. 1988. A world revision of Strobilomyia gen.n.: the anthomyiid seed pests of conifers (Diptera: Anthomyiidae) Syst. Entomol. 13: 271-314.

Miller, G.E. 1986. distribution of Contarinia oregonensis Foote (Diptera: Cecidomyiidae) eggs in Douglas-fir seed orchards and a method of estimating egg density. Can. Entomol. 118:1291-1295.

Pollard, D.F.W. 1982. Canadian national list of seed orchards, 1981. Can. For. Serv., Inf. Rep. DPC-X-13.

Rauf, A. & D.M. Benjamin. 1983. Spatial distribution of jack pine cones and those attacked by insects. Great Lakes Entomol. 16: 183-185.

Rauter, R.M. & B.J. Graham. 1983. The genetics and tree improvement of larches in Ontario. pp. 11-27, **IN:** Larch symposium: potential for the future. Univ. Toronto and Ontario Min. Nat. Res., Toronto, Ontario.

Roques, A. (in press). The larch cone fly in the French Alps. pp 1-28, **IN:** A.A. Berryman (ed.) Population dynamics of forest insects. Plenum Press, N.Y.

Roques, A., A. Martinez, & A. Delplanque. 1983. Les Diptères Anthomyiidae du genre Lasiomma Stein, ravageurs des cones et graines du Mélèze d'Europe (Larix decidua Mill.) en France I. Taxonomie et Répartition. J. Appl. Entomol. 95: 429-439.

Roques, A., J.P. Raimbault, & A. Delplanque. 1984. Les Diptères Anthomyiidae du genre Lasiomma Stein, ravageurs des cones et graines du Mélèze d'Europe (Larix decidua Mill.) en France II. Cycles biologiques et dégâts. J. Appl. Entomol. 98: 350-367.

Ruesink, W.G. & M. Kogan. 1975. The quantitative basis of pest management: sampling and measuring. pp 309-335, **IN:** Metcalf R.L. & W.H. Luckman (eds). Introduction to insect pest management. John Wiley & Sons, N.Y.

SAS Institute. 1985. SAS user's guide: statistics, version 5 ed. Cary, N.C.

Simpson, J.D. 1983. The New Brunswick tree improvement council's breeding strategy for tamarack. pp. 219-224, **IN:** Proceedings 28th Northeastern tree improvement Conference. Univ. New Hampshire, Durham.

Stadnitsky, G.V., V.P. Grebenshchikova, F.V. Naumov & A.M. Bortnik. 1974. Counting, Observing and Forecasting pests of the reproductive organs of coniferous trees and controlling these pests in seed orchards and plantations in the European USSR: Provisional Practical recommendations (Translated from Russian). 73pp.

Tosh, K.J. 1986. Development and distribution of cones, pollination, and yield of seeds in young plantations of Tamarack. M.Sc.F. dissertation, University of New Brunswick.

Tripp, H.A. 1954. The instars of a maggot (Pegohylemyia) inhabiting white spruce cones. Can. Entomol. 86: 184-189.

Tripp, H.A., & A.F. Hedlin. 1956. An ecological study and damage appraisal of white spruce cone insects. For. Chron. 32: 400-410.

TECHNICAL SESSION IV:

Insect Control

Moderator: Dr. Willard Fogal, Chalk River, Ontario, CANADA

PROMISING NEW PESTICIDES FOR CONE AND SEED INSECT CONTROL IN THE SOUTHERN UNITED STATES

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SUMMARY

Azinphosmethyl, chlorpyrifos, bifenthrin, and Bacillus thuringiensis (B.t.) applied with a high-volume sprayer were evaluated for cone and seed insect control in a loblolly pine seed orchard in Texas during 1986. Six high-volume bifenthrin and chlorpyrifos sprays applied monthly provided insect control comparable to that of the azinphosmethyl standard. Compared to no treatment, B.t. significantly reduced damage by coneworms and seedworms, but not by seed bugs. A second study was conducted during 1987 to compare three and six high volume bifenthrin sprays with six applications of both fenvalerate and esfenvalerate. Fenvalerate, esfenvalerate, and bifenthrin applied six times were highly effective against coneworms and seed bugs. Bifenthrin applied three times significantly reduced insect damage compared to the untreated check, but was less effective for seed bug control than the six applications. The influence of these treatments on populations of several homopteran insect species also was documented. Factors affecting future use of insecticides and potential new insecticide products and strategies are discussed.

Key Words: bifenthrin, esfenvalerate, fenvalerate, Dioryctria, Leptoglossus, Chionaspis, Oracella, Toumeyella, seed orchard efficiency.

INTRODUCTION

Primary pests of pine seed orchards in the southern United States include four species of coneworms, Dioryctria spp., the leaffooted pine seed bug, Leptoglossus corculus (Say), and the shieldback pine seed bug, Tetyra bipunctata (Herrich-Schaffer). These insects cause severe losses to potential seed crops in unprotected southern pine seed orchards (Fatzinger et al. 1980). Currently, azinphosmethyl (Guthion®), carbofuran (Furadan®), esfenvalerate (Asana®), fenvalerate (Pydrin®), and permethrin (Ambush®, Pounce®) are registered for the control of coneworms and seed bugs in southern pine seed orchards.

Carbofuran, a granular systemic, is convenient to apply and is particularly effective against early season seed bug damage, but it does not last all season, provides inadequate control of coneworms, and may cause

adverse impacts on the environment. Azinphosmethyl, used to control cone and seed insects in seed orchards for more than 20 years, remains the most widely used insecticide. However, its high mammalian toxicity and strong odor preclude use in some environmentally-sensitive areas.

Fenvalerate, a pyrethroid, is relatively safe to use and has a long residual. However, high infestation levels of several homopteran insects frequently develop following repeated applications of fenvalerate in pine seed orchards (Texas Forest Service 1980, 1984; DeBarr et al. 1982). Increased populations of the pine tortoise scale, Toumeyella parvicornis (Cockerell), the striped pine scale, T. pini (King), the wooly pine scale, Pseudophillippia quaintancii Cockerell, and a mealybug, Oracella acuta (Lobdell), have been noted in southern pine seed orchards following fenvalerate applications. Permethrin, also a pyrethroid, has a particularly low mammalian toxicity, but has a shorter residual than fenvalerate and has been used little in seed orchards.

Esfenvalerate has a purified form of the active ingredient in fenvalerate and is expected to perform similar to fenvalerate at one-quarter the rate. It also is expected to produce the same undesirable effects on homopteran insect populations as fenvalerate. However, esfenvalerate has not been tested for cone and seed insect control in southern pine seed orchards.

New insecticide products are needed to compensate for the disadvantages of those currently in use and to replace products which may be discontinued in the future. Insecticides chosen for field evaluation during 1986 and 1987 included chlopyrifos, bifenthrin, esfenvalerate, and Bacillus thuringiensis. Chlorpyrifos, an organophosphate, was selected because it already is registered for many forestry uses including control of scale insects; it has a relatively low mammalian toxicity and was highly toxic to D. amatella larvae in laboratory bioassays (DeBarr and Fedde 1980). Bifenthrin is a new pyrethroid applied at low rates and has a particularly broad spectrum of activity including lepidopterous larvae, mealybugs, whiteflies, and mites. Esfenvalerate was included in field evaluations to confirm its efficacy for cone and seed insect control. Bacillus thuringiensis (B.t.) is an environmentally-safe microbial insecticide widely used in forestry which has shown promise against coneworm larvae on loblolly pine in Arkansas (Gage 1975; McLeod et al. 1984).

High volume ground sprays of bifenthrin, chlorpyrifos, and azinphosmethyl provided excellent control of coneworms, seedworms, and seed bugs in a loblolly pine seed orchard in Texas during 1986 (Cameron et al. 1987). An emulsifiable concentrate formulation of bifenthrin (Capture®) applied at a low rate (0.01% a.i.) was consistently the best treatment. Chlorpyrifos was less effective than azinphosmethyl and bifenthrin for controlling seed bugs. Bacillus thuringiensis applied 11 times at bi-weekly intervals significantly reduced coneworm and seedworm damage, but was less effective than the three conventional insecticides for coneworm control, and did not reduce seed bug damage. Sucking insect outbreaks were not associated with any of the treatments in this test.

In a separate test conducted in Georgia during 1986, low volume aerial applications of chlorpyrifos (Dursban® 4E) in an emulsifiable concentrate formulation did not effectively control coneworms or seed bugs (Cameron et al. 1987). Chlorpyrifos residues on foliage apparently were below levels necessary for significant insect control. Aerial applications at the same rate of chlorpyrifos in a wettable powder formulation provided four times the residues in 1987 compared to those detected in the 1986 test.

Insecticides selected for testing in 1987 were fenvalerate, esfenvalerate, and a wettable powder formulation of bifenthrin. Since fenvalerate appears to control cone and seed insects for up to eight weeks (William Lowe, Western Gulf Forest Tree Improvement Program, personal communication) and bifenthrin applied six times at monthly intervals provided nearly total protection of cones and seeds in the 1986 test, a comparison of bifenthrin applied at four- and eight-week intervals also was included in the 1987 test.

METHODS

Four insecticide treatments and an unprotected check were evaluated in a 12-year-old loblolly pine seed orchard near Kirbyville, Texas, in an area left untreated during 1986 and 1987. Fenvalerate (Pydrin®) served as a standard treatment and was applied at the recommended rate (0.025% a.i.). Esfenvalerate (Asana® 1.9EC) was used at one-fourth the rate of fenvalerate, 0.006% a.i., and bifenthrin (Talstar® 10WP) was applied at 0.01% a.i. These three insecticides were applied six times at 4-week intervals from April through September in 1987 as follows: April 20, May 18, June 23, July 21, August 20, and September 21. In a separate treatment, bifenthrin (0.01% a.i.) was applied three times at 8-week intervals on April 20, June 23, and August 20. Individual trees were sprayed with a hydraulic sprayer to the point of runoff (ca. 8 gal/tree). The wettable powder bifenthrin formulation used in this test was somewhat difficult to mix and required preparing a slurry in a separate container before pouring it into the tank to avoid clogging the filter screen in the sprayer.

Experimental design, treatment evaluation, and data analysis in this test were identical to procedures used in the previous year's study (Cameron et al. 1987) and similar to those described in detail by Nord et al. (1984). Five of nine clones in the orchard were selected on the basis of size of the conelet and cone crops and the frequency of occurrence in the orchard. Only trees with more than 60 conelets and cones were included in the population of test trees. Treatments were randomly assigned to two ramets per clone. Two trees from separate clones were destroyed by a tornado during the study, leaving 48 instead of the original 50 test trees. The distance between test trees was at least 20 m to minimize potential effects of drift. All other trees in the orchard were left untreated. Variables measured to evaluate treatment effects included: 1) April-October survival and mortality by cause among a minimum of 60 tagged conelets and cones per tree, and 2) seed quality factors (Bramlett et al. 1977) from 10 conelets and 10 cones harvested from each tree in October.

Test trees were inspected for the occurrence of homopteran insect populations in October 1987 and relative population levels of T. parvicornis, T. pini, O. acuta, and Chionaspis heterophyllae (Cooley), the pine needle scale, were estimated using the following infestation scoring system: 0 = none, 1 = few insects on scattered branches, 2 = many branches with few insects, or few branches with moderate to large numbers of insects, and 3 = many branches with many insects. In March 1988, branch samples were collected from each test tree at ca 7 m at the four cardinal directions. Samples consisting of 30 cm of needle bearing branch were taken to the laboratory for inspection. All scale insects and mealybugs on each branch and on 50 randomly-selected needle bundles were recorded.

Data were analyzed by the General Linear Model (SS4) and Duncan's New Multiple Range Test procedures using the Statistical Analysis System (Ray 1982). Treatments were assumed to be fixed while clones and ramets within clones were assumed to be random effects in a mixed linear model. Only those variables which had significant F values ($P<0.05$) for treatments were subjected to Duncan's New Multiple Range Test. Percentage data were transformed using the arc sine square root transformation.

RESULTS AND DISCUSSION

Cone and Seed Insect Control

Significant differences among treatment means ($P<0.05$) were observed for all conelet and cone survival and damage factors (Table 1) and seed quality factors (Table 2), except other cone mortality, seedworm damage, empty seeds, and abnormal seeds. Fenvalerate, esfenvalerate, and bifenthrin treatments applied six times all provided excellent and comparable insect control. In general, the three application bifenthrin treatment was far less effective than the six application treatments, but three sprays significantly reduced insect damage compared to that on unprotected check trees.

Coneworm damage to conelets and cones was significantly reduced by all four insecticide treatments, but none of the treatments completely eliminated coneworm damage to second-year cones. Although three applications of bifenthrin were as effective as six for coneworm control in this test, seed bug feeding resulted in significantly higher conelet mortality (9.2%), ovule abortion in conelets (26.2%), and seed bug damage in cones (10.1%) on trees treated only three times. Yet, no significant differences ($P>0.05$) in numbers of filled seeds in cones were observed among the four insecticide treatments.

Substantial proportions of the second-year cones and seeds were lost to "other losses" (5-6%) and empty seeds (13-18%), respectively. But losses attributed to these two damage types did not vary significantly ($P>0.05$) among treatments. Many of the cones classified as "other losses" in this study may have been infected by the fungus Fusarium moniliforme Shield. var. subglutinans Wollenw. & Reink. (Sutherland et al. 1987). Similar proportions of empty seeds were encountered in this orchard in 1986 and 1987 (16.6% and 15.0%, respectively). Much of this loss may be associated with lethal gene combinations inherent to this orchard (Bramlett et al. 1977).

Table 1. Mean percent survival, coneworm damage, and other losses among conelets and cones on trees treated with high volume insecticide sprays or left unprotected in a loblolly pine seed orchard near Kirbyville, TX, during 1987.

Treatment[1]	Conelets			Cones		
	Apr-Oct survival	Coneworm damage	Other losses	Apr-Oct survival	Coneworm damage	Other losses
Fenvalerate (6X)	98.3a[2]	0.2ab	1.5a	89.4a	5.2a	5.4a
Esfenvalerate (6X)	98.5a	0.0a	1.5a	87.8a	6.1a	6.1a
Bifenthrin (6X)	97.4a	0.4ab	2.2a	89.3a	5.0a	5.7a
Bifenthrin (3X)	90.8b	1.1b	8.0b	86.9a	7.8a	5.2a
Unprotected	73.1c	3.4c	23.4c	78.0b	17.3b	4.7a

1 Formulations (rates) of insecticide treatments (number of applications) listed in this table were Pydrin® 2.4EC (0.025% a.i.), Asana® 1.9EC (0.006% a.i.), Talstar® 10WP (0.01% a.i.), respectively.

2 Means within each column followed by the same letter are not significantly different (P>0.05, ANOVA, Duncan's Multiple Range Test).

Table 2. Mean percentages for seed quality factors on trees treated with high volume insecticide sprays or left unprotected in a loblolly pine seed orchard near Kirbyville, TX, during 1987.

Treatment[1]	Conelets	Cones				
	Sound ovules	Filled seed	2nd-yr aborted ovules	Seed bug damage	Seedworm damage	Total insect damage
Fenvalerate (6X)	94.1a	84.9a	0.7a	0.9a	0.0a	1.7a
Esfenvalerate (6X)	93.9a	83.6a	0.8a	0.9a	0.0a	1.7a
Bifenthrin (6X)	91.2a	75.1a	2.0a	3.4a	0.2a	5.6a
Bifenthrin (3X)	73.8b	75.2a	2.4a	7.7b	0.7a	10.8b
Unprotected	62.6c	45.5b	17.5b	20.3c	0.4a	38.2c

1 Insecticide treatments and statistical analyses as in Table 1.

The techniques developed for monitoring seed production efficiency for southern pine seed orchards serve to illustrate the relative effectiveness of insecticide treatments (Godbee et al. 1977; Bramlett and Godbee 1982). The effects of insecticides on seed orchard efficiency for a two-year cone crop can be simulated in one season by combining the efficiency (survival) figures for conelets and cones obtained in a one year test (Figure 1). Seed orchard efficiency was similar for each of the insecticides when applied six times, fenvalerate (70.2%), esfenvalerate (67.9%), and bifenthrin (59.6%). Efficiency was 43.8% for bifenthrin applied three times and 16.2% for the unprotected check trees.

By comparison, seed orchard efficiencies obtained from the 1986 insecticide test (Cameron et al. 1987) were azinphosmethyl, 76.2%; bifenthrin, 81.3%; chlorpyrifos, 72.1%; B. thuringiensis, 42.6%; and unprotected check, 42.0%. Thus, the 1987 tests were more rigorous in terms of insect population levels and resulting damage on unprotected trees.

Effects on Homopteran Insect Populations

Four species of sucking insects were observed on treatment trees in October 1987, including: T. parvicornis, T. pini, C. heterophyllae, and O. acuta. Population levels for these insects were estimated visually as sample cones were harvested from treatment trees in October. Mean infestation

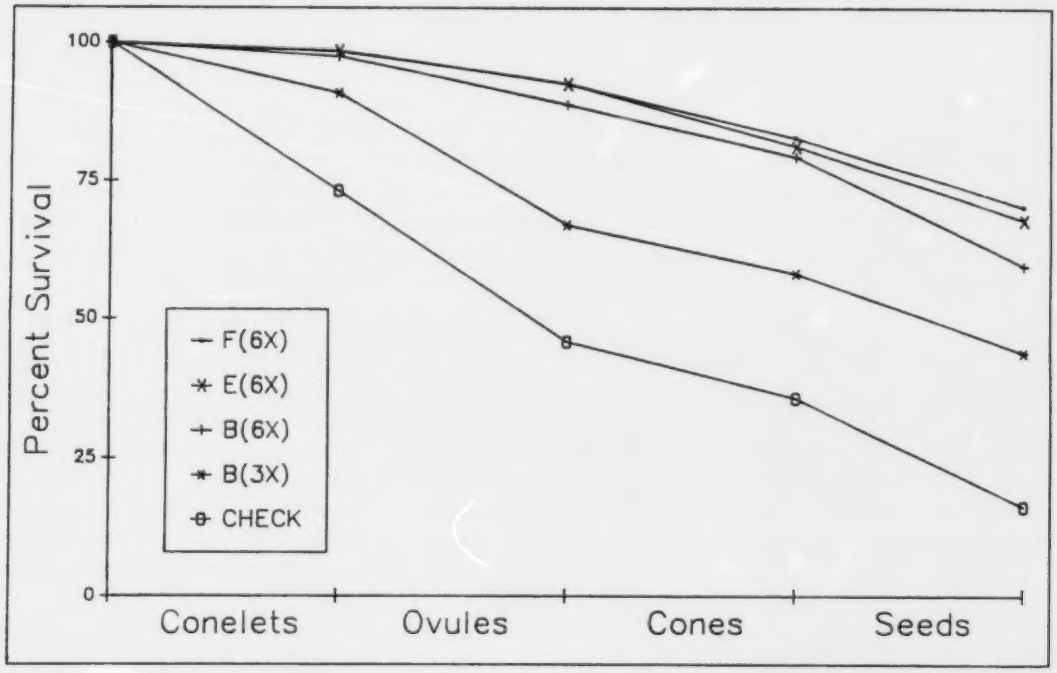

Figure 1. Seed orchard efficiency curves for four insecticide treatments (F(6X) - six applications of fenvalerate, E(6X) - six applications of esfenvalerate, B(6X) - six applications of bifenthrin, B(3X) - three applications of bifenthrin) and an unprotected check in a loblolly pine seed orchard near Kirbyville, TX, during 1987.

scores based on these observations are presented in Table 3. Toumeyella pini was relatively scarce and therefore the data were combined with that for T. parvicornis. These results indicate that Toumeyella scale populations were higher on the fenvalerate-treated trees than on trees treated with other insecticides. Chionaspis heterophyllae populations may have been higher on bifenthrin (6X) treated trees, but were absent on the trees treated with fenvalerate and esfenvalerate. Conversely, O. acuta populations appeared to have increased on the esfenvalerate- and fenvalerate-treated trees and were eliminated by the bifenthrin sprays.

The numbers of C. heterophyllae and O. acuta present on branch samples collected in March 1988 are presented in Table 4. Toumeyella scales were no longer present in significant numbers on treatment trees in March. These data confirmed that numbers of C. heterophyllae were significantly higher ($P<0.05$) on the bifenthrin treated trees than on the check trees. Oracella acuta populations were in the crawler stage mainly inside the needle fascicle bundle sheaths in early March. They were almost absent from bifenthrin-treated trees, but were present in comparable numbers on the other treatments.

The few apparent differences in sucking insect populations detected on the branch samples compared to those determined from the previous visual survey may be due to actual insect population changes during the five month interval between samples, or due to experimental error. At low population levels, distributions of T. parvicornis and C. heterophyllae are clumped (very numerous on widely scattered branches); thus sampling error is large.

Table 3. Mean infestation scores for Toumeyella spp., Chionaspis heterophyllae (Cooley), and Oracella acuta (Lobdell), on test trees following insecticide treatments in a loblolly pine seed orchard near Kirbyville, TX, October 1987.

Treatment[1]	Mean + SD infestation score[2]		
	Toumeyella spp.	Chionaspis heterophyllae	Oracella acuta
Fenvalerate (6X)	1.3 ± 1.2	0	1.4 ± 1.4
Esfenvalerate (6X)	0.5 ± 0.7	0	1.0 ± 0.9
Bifenthrin (6X)	0.7 ± 0.7	0.9 ± 1.3	0
Bifenthrin (3X)	0	0.1 ± 0.3	0
Check	0.5 ± 0.5	0.2 ± 0.4	0.1 ± 0.3

1 Insecticide treatments as in Table 1.

2 Infestation scores based on visual observation of each treatment tree as follows: 0 = none, 1 = few insects on scattered branches, 2 = many branches with few insects, or few branches with moderate to large numbers of insects, 3 = many branches with many insects.

Table 4. Mean numbers of Chionaspis heterophyllae (Cooley) and Oracella acuta (Lobdell) on branch and needle samples following insecticide treatments in a loblolly pine seed orchard near Kirbyville, TX, March 1, 1988.

Treatment[1]	Chionaspis heterophyllae	Oracella acuta
Fenvalerate (6X)	0.3 b	13.1 a
Esfenvalerate (6X)	20.0 b	17.8 a
Bifenthrin (6X)	101.0 a	0.2 b
Bifenthrin (3X)	160.6 a	0.0 b
Unprotected	33.6 b	16.6 a

[1] Insecticide treatments and statistical analyses as in Table 1.

CONCLUSIONS

Fenvalerate, esfenvalerate, and bifenthrin applied six times in 1987 were highly and comparably effective in preventing losses to cone and seed insects. Each of these treatments increased seed yields about four fold compared to unprotected checks. Three applications of bifenthrin were inferior to six applications mostly due to increased seed bug damage. Yet this treatment increased seed orchard efficiency 2.7 times compared to the unprotected checks, illustrating that substantial gains can be attained with less frequent spraying.

Based on two seasons of testing, bifenthrin remains a good candidate for registration for seed orchard insect control. The emulsifiable concentrate formulation (Capture®) would be easier to handle and may be slightly more effective than the wettable powder formulation (Talstar®). Further testing is needed to confirm the efficacy of bifenthrin applied as a low volume aerial spray in pine seed orchards.

Responses of homopteran insect populations varied by species and insecticide treatment. Fenvalerate and esfenvalerate generally had similar effects on sucking insect populations. Pine needle scale populations appeared to decrease on fenvalerate- and esfenvalerate-treated trees and increase on bifenthrin-treated trees. Conversely, mealybug populations were the same or possibly increased on fenvalerate- and esfenvalerate-treated trees compared to check trees, but where nearly absent on trees treated with bifenthrin. These differential effects of insecticides among sucking insect species demonstrate the complexities associated with secondary pests.

A LOOK TO THE FUTURE

The use of pesticides in pine seed orchards may be altered dramatically in the future. Factors which may affect insecticide registrations and use include: 1) continued and new problems with induced pests, 2) insect resistance to insecticides, 3) restrictions and cancellations of registered pesticide uses, 4) increased regulations on use regarding water quality, inert ingredients, endangered species protection, and farm worker protection, and 5) increased difficulty in obtaining new registrations.

Some new approaches currently used in agriculture which might provide opportunities for pest management in southern pine seed orchards include the use of: 1) tank mixes such as an organophosphate with a pyrethroid at lower concentrations, 2) synergists with pyrethroids, 3) ULV applications with vegetable oil for maintaining constant droplet size and better penetration of sprays, and 4) early sprays with less insecticide when life stages are synchronized and populations are low.

In the near future new pesticide products for pine seed orchards are likely to be new pyrethroids. However, much of current research in pest management is focused on developing completely new families of insecticides, genetic manipulation of hosts and microbials, such as Bacillus thuringiensis, and the use of other biological control agents. This research may produce revolutionary new means of managing pest problems.

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LITERATURE CITED

Bramlett, D. L., E. W. Belcher, Jr., G. L. DeBarr, G. D. Hertel, R. P. Karrfalt, C. W. Lantz, T. Miller, K. D. Ware, and H. O. Yates, III. 1977. Cone analysis of southern pines - a guide book. USDA For. Ser. Gen. Tech. Rep. SE-13. 28 pp.

Bramlett, D. L. and J. F. Godbee, Jr. 1982. Inventory-monitoring system for southern pine seed orchards. Georgia For. Res. Paper 28. 17 pp.

Cameron, R. S., G. L. DeBarr, J. F. Godbee, and J. W. Taylor. 1987. Potential alternative insecticides for insect control in southern pine seed orchards. pp. 182-189. In Proc. Nineteenth Southern Forest Tree Improvement Conference, College Station, TX.

DeBarr, G. L. and V. H. Fedde. 1980. Contact toxicity of 17 insecticides to larvae of Dioryctria amatella (Lepidoptera: Pyralidae). Can. Entomol. 112: 521-523.

DeBarr, G. L., L. R. Barber, M. S. McClure, and J. C. Nord. 1982. An assessment of the problem of scale and mealybug outbreaks associated with the use of insecticides in southern pine seed orchards. Unpublished USDA Forest Service Report. Athens, GA. 57 pp.

Fatzinger, C. W., G. D. Hertel, E. P. Merkel, W. D. Pepper, and R. S. Cameron. 1980. Identification and sequential occurrence of mortality factors affecting seed yields of southern pine seed orchards. USDA For. Ser. Res. Pap. SE-216. 43 pp.

Gage, E. V. 1975. Evaluation and timing of selected insecticides for control of Dioryctria coneworms in a loblolly pine seed orchard. M. S. thesis, Univ. of Arkansas, Fayetteville. 28 pp.

Godbee, Jr., J. F., T. S. Price, and D. L. Bramlett. 1977. Effect of an insecticide spray program on slash pine seed orchard efficiency. pp. 108-115. In Proc. Fourteenth Southern Forest Tree Improvement Conference, Gainesville, FL.

McLeod, P. J., W. C. Yearian, and S. Y. Young. 1984. Evaluation of Bacillus thuringiensis for coneworm, Dioryctria spp., control in southern pine seed orchards. J. Georgia Entomol. Soc. 19: 408-413.

Nord, J. C., G. L. DeBarr, N. A. Overgaard, W. W. Neel, R. S. Cameron, and J. F. Godbee. 1984. High-volume applications of azinphosmethyl, fenvalerate, permethrin and phosmet for control of coneworms (Lepidoptera: Pyralidae) and seed bugs (Hemiptera: Coreidae and Pentatomidae) in southern pine seed orchards. J. Econ. Entomol. 77: 1589-1595.

Ray, A. J. (ed). 1982. SAS Users' Guide: Statistics. SAS Institute, Cary, North Carolina. 584 pp.

Sutherland, J. R., T. Miller, and R. S. Quinard, (eds). 1987. Cone and seed diseases of North American conifers. North American Forestry Commission. Publ. No. 1. 77 pp.

Texas Forest Service. 1980. Texas forest pest activity 1978-79 and Forest Pest Control Section biennial report. Tex. For. Serv. Publ. 121. 21 pp.

Texas Forest Service. 1984. Texas forest pest report 1982-83. Tex. For. Serv. Publ. 136. 31 pp.

TIMING OF ACEPHATE IMPLANTS FOR CONTROL OF THE COASTAL SEED INSECT COMPLEX OF DOUGLAS-FIR IN NORTHERN CALIFORNIA[1]

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SUMMARY

To reduce seed and cone insect damage, 0.875 g per capsule of acephate (technical grade) was implanted into individual Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, trees on 15 April or 6 May. A spacing of one capsule per 10 cm of trunk circumference was used. Implant treatments had no direct effect on infestations of the Douglas-fir cone gall midge, Contarinia oregonensis Foote, or the Douglas-fir seed chalcid, Megastigmus spermotrophus Wachtl. Both implant treatments, however, significantly reduced the damage of the fir coneworm, Dioryctria abietivorella (Grote), and the Douglas-fir cone moth, Barbara colfaxiana (Kearfott), by at least 62%. The later implant significantly increased the number of filled seeds per cone by 154% compared with control trees, with no significant difference between implant treatment dates. Interaction between reduction of damage by Lepidoptera and the increase in gall midge-damaged seeds and filled seeds suggests a reciprocal association with reduced predation.

Key Words: Pseudotsuga menziesii, cone and seed insects, trunk implants

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[1]Trade names and commercial products and enterprises are mentioned solely for information. No endorsement by the U.S. Department of Agriculture is implied.

INTRODUCTION

The Douglas-fir cone moth [Barbara colfaxiana (Kearfott)], the fir coneworm [Dioryctria abietivorella (Grote)], the Douglas-fir cone gall midge [Contarinia oregonensis Foote], and the Douglas-fir seed chalcid [Megastigmus spermotrophus Wachtl] are a serious pest complex of Douglas-fir seed crops in northern California. Larvae of the gall midge infest scales and interfere with ovule development and seed extraction. Larvae of the cone moth and the coneworm destroy both seeds and cone scales. Larval development of seed chalcids occurs within a single seed and affects only one seed (Hussey 1955, Hedlin et al. 1980).

Previous efforts to control of one or more of these these insects with application of insecticide sprays on the Douglas-fir tree canopy has yielded mixed results (Miller 1984). Oxydemeton-methyl (designated as Inject-A-Cide®) injected into Douglas-fir trees killed insects attacking cones and increased seed yield (Koerber 1979, Johnson et al. 1984), and technical-grade acephate implants (designated as Acecap®) were effective against the western spruce budworm [Choristoneura occidentalis Freeman] and the spruce coneworm [Dioryctria reniculelloides Mutuura and Munroe] in Idaho and Montana (Reardon & Haskett 1981, Reardon et al. 1985).

This paper reports the results of implanting acephate at different times in the spring for control of the coastal cone and seed insect complex found on Douglas-fir in northern California.

METHODS

Two treatment schedules and a control were designated for cone-bearing trees on the Klamath National Forest in northern California. An early implant treatment (15 April) coincided with flower bud opening, the late implant treatment (6 May) with cones turning pendant, and a control. Acecap® capsules were implanted by using the procedure described previously (Reardon et al. 1985).

For our study, 105 Douglas-fir trees that ranged from 30 to 40 m in height were arbitrarily selected and numbered. The three treatments were assigned at random, and the experiment was arranged in completely randomized design. Subsequent frost damage reduced the number of cone-bearing trees from 105 to 31, resulting in an unbalanced design with 6, 12, and 13 replicates for early implants, late implants, and control treatments, respectively.

In the fall, mature cones were harvested and 10 cones from each tree were randomly selected. Each cone was dissected and the number of aborted seeds and the number of seeds affected by gall midge, cone moth, and coneworm were recorded. Extractable seeds from each cone were placed in a labeled envelope. Each envelope was radiographed to determine the number of seeds that were aborted, filled, empty, or affected by specific insects. Seed assessment categories were analyzed as proportions of the total possible seeds per cone.

General linear models (GLM) program was used to analyze data (SAS Institute 1982). Bonferroni's multiple comparison procedure was used to make pairwise comparisons of differences in treatment least square means with an unbalanced design (Milliken & Johnson 1984).

RESULTS AND DISCUSSION

The mean number of aborted seeds per cone ranged from 9.6 for controls to 13.6 for early implants, with no significant difference between treatments and control. The mean number of insect-damaged seeds decreased from 26.7 to 15.2 seeds for late implants, representing a statistically significant reduction of 25.8% (Fig. 1). The 19.8% increase in the mean percent of extractable seeds for the late implant treatment was also statistically significant (Fig. 1).

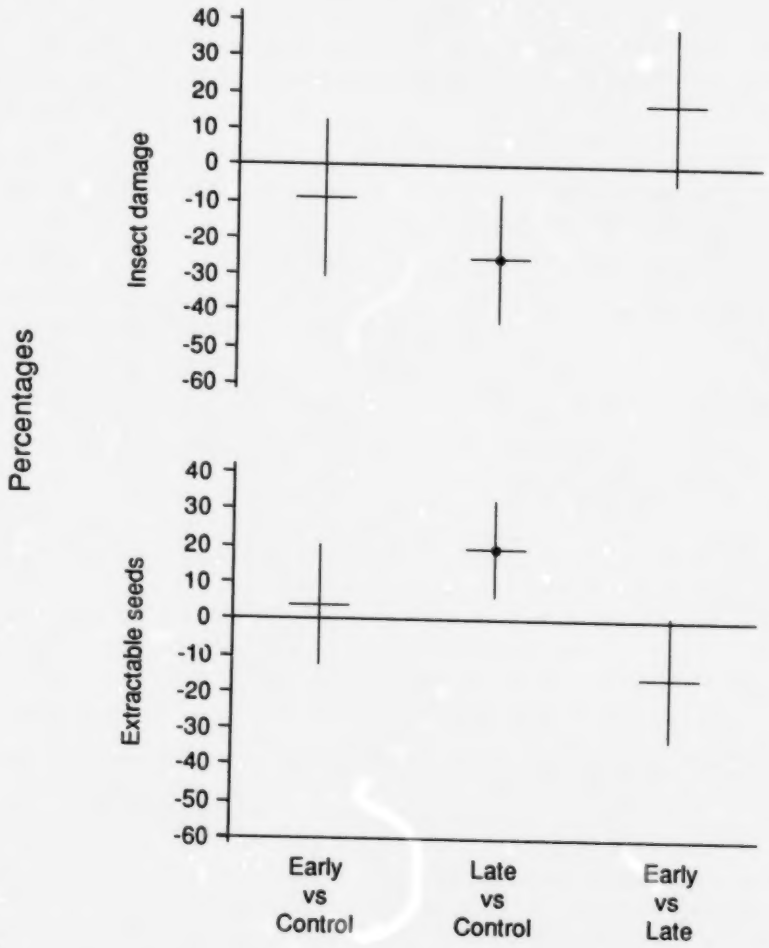

Figure 1. Mean difference in percentage of overall insect damage and extractable seeds. Vertical line segments, 95% CI; ●, significant difference from zero with an overall error rate of at most $\alpha = 0.05$.

Acephate implants reduced damage by both lepidoptera species (Table 1). Mean percentages of seeds damaged by fir coneworm and cone moth were significantly less than the untreated controls for both early and late applications. There were no significant differences in seeds damaged by either fir coneworm or cone moth between the early and late application dates (Fig. 2). There was no significant reduction in seed chalcid infestation associated with either acephate treatments (Fig. 2). The mean percentage of gall midge-damaged seeds for early implants (30.9%) was 259.3±125.9% (X±SEM) greater than that for the untreated controls (8.6%) (Table 1). This difference represents a significant increase in the number of seeds damaged by the gall midge in the early implant treatment compared with both the late implant treatment and untreated control trees (Fig. 2). The mean difference of filled and unfilled seeds indicated a significant increase for the late implant treatment, with no significant difference associated with early timing (Fig. 2).

Table 1. Percent insect damage and seed yield of Douglas-fir cones on acephate trunk-implanted trees.

Assessment Category	Treatment (X%±SEM)[a]		
	Early n=6	Late n=12	Control n=13
	%		
B. colfaxiana	8.4 (4.6)	10.3 (3.3)	31.4 (3.1)
D. abietivorella	5.2 (2.5)	2.0 (1.8)	13.5 (1.7)
C. oregonensis	30.9 (4.0)	15.5 (2.9)	8.6 (2.8)
M. spermotrophus	3.8 (1.7)	7.2 (1.2)	5.6 (1.2)
Unfilled	21.5 (4.0)	32.0 (2.8)	19.3 (2.7)
Aborted	23.6 (3.9)	24.3 (2.8)	18.4 (2.7)
Filled	7.2 (1.3)	8.9 (0.9)	3.5 (0.9)

[a] Means are least square means in Statistical Analysis System (SAS Institute 1982).

The early treatment reduced overall insect damage 18.3% and the late treatment reduced damage 40.8%. Both treatments resulted in substantial increases in seed yield. The late treatment was most effective with 154% increase in filled seed per cone. We attribute the increase in seed yield to reduction in damage by the Douglas-fir cone moth and fir coneworm. Further interpretation of the results is difficult due to strong interactions among the four species of insects infesting the cones (Stein & Markin 1986). The larvae of the cone moth and fir coneworm consume and destroy seeds that would otherwise be attributed to damaged by larvae of the gall midge and seed chalcid. As a result, reduction of damage by one species may result in an apparent increase in damage by another (Stein et al. 1988). In our study, the early implant treatment increased seed damage by the cone gall midge

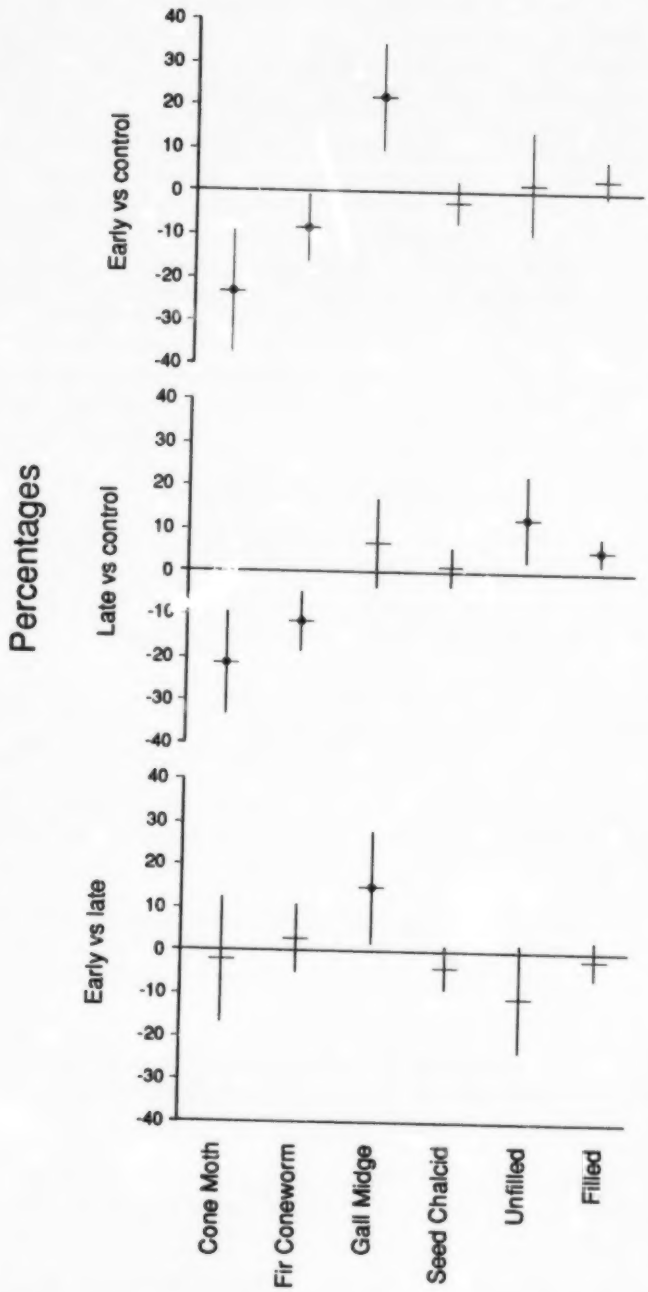

Figure 2. Mean difference in percentage of insect damage, filled and unfilled seed. Vertical line segments; 95% CL; ●, significant difference from zero with an overall error rate of at most $\alpha = 0.05$.

significantly (259.3 ± 125.9%). The numbers of unfilled seeds also increased. We attributed these increases to reduction in numbers of seeds per cone destroyed by larvae of the two species of lepidoptera. There was also an indication that increases in numbers of aborted seeds were associated with reduction in insect damage. Increased aborted and unfilled seeds would be expected to reflect their proportion of occurrence in the cone. However, differences in species distribution of feeding activity within the cone (Volney 1984, Rappaport & Volney 1989), may result in higher numbers of unfilled and aborted seeds in portions of the cone with less insect damage.

In summary, acephate implants substantially decreased damage by the Douglas-fir cone moth and fir coneworm, but apparently did not reduce damage by the cone gall midge or seed chalcid. Both the early and late treatments resulted in increased seed yield. It would be desirable to conduct further tests to determine the effect of acephate implants on the gall midge and seed chalcid. European entomologists have an excellent opportunity to conduct tests of this control method against the Douglas-fir seed chalcid in the absence of the other North American insects.

LITERATURE CITED

Hedlin, A.F., Yates III, H.O., Tovar, D.C., Ebel, B.H., Koerber, T.W. and Merkel, E.P., 1980: Cone and seed insects of North America conifers. Canadian Forestry Serv., For. Serv. U.S. Dept. Agric., and Secretaria de Agricultura y Recursos Hidraulicos, Mexico. 122 pp.

Hussey, N.W., 1955: The life histories of Megastigmus spermotrophus Wachtl (Hymenoptera:Chalcididae) and its principal parasite, with descriptions of the development stages. Trans. R. Ent. Soc., vol. 106, pp. 133-151.

Johnson, D.R., Markin, G.P., Reardon, R.C. and Randall, W.K., 1984: Injecting Metasystox-R at three spacing intervals to improve seed yield in Douglas-fir. Jour. Econ. Entomol., vol. 77, pp. 1320-1322.

Koerber, T.W., 1979: Bole injected systemic insecticides for control of Douglas-fir cone insects. In: Proceedings of a Symposium on Systemic Chemical Treatments in Tree Culture; 9-11 Oct. 1978; East Lansing, Michigan, pp. 295-302.

Miller, G.E., 1984: Pest management in Douglas-fir seed orchards in British Columbia. In: Proceedings of the Cone and Seed Insects Working Party Conference (S2.07-01); 31 July-6 Aug. 1983; Athens, Georgia, pp. 179-185.

Milliken, G.A. and Johnson, D.E., 1984: Analysis of messy data. Volume 1: Designed experiments. Lifelong Lifetime Learning Publications, Belmont, California. 600 pp.

Rappaport, N.G. and Volney, W.J.A., 1989: Effect of pest species exclusions in Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) cone and seed insects: Implications for pest management. In: Proceedings of the Cone and Seed Insects Working Party Conference (S2.07-01); 27-30 June 1988; Victoria, B.C. (In Press)

Reardon, R.C. and Haskett, M.J., 1981: Effect of Orthene medicaps on

populations of western spruce budworm on grand fir and Douglas-fir. Jour. Econ. Entomol., vol. 74: pp. 266-270.

Reardon, R.C., Barrett, L.J., Koerber, T.W., Stipe, L.E. and Dewey, J.E., 1985: Implantation and injection of systemics to suppress seed and cone insects in Douglas-fir in Montana. Can. Entomol., vol. 117, pp. 961-969.

SAS Institute, 1982: SAS user's guide: Statistics. SAS Institute, Cary, N.C.

Stein, J.D. and Markin, G.P., 1986: Evaluation of four chemical insecticides registered for control of the Douglas-fir cone gall midge, Contarinia oregonensis (Diptera:Cecidomyiidae), and the Douglas-fir seed chalcid, Megastigmus spermotrophus (Hymenoptera:Torymiidae), in Douglas-fir seed orchards. Can. Entomol., vol. 118, pp. 1185-1191.

Stein, J.D., Koerber, T.W. and Frank, C.L., 1988: Trunk-implanted Acephate to Protect Douglas-fir Seed Croups on Individual Trees in Northern California. Jour. Econ. Entomol. (In Press)

Volney, W.J.A., 1984: Competition and survival among insects colonizing Douglas-fir (Pseudotsuga menziesii [Mirb.] Franco) cones. In: Proceedings of the Cone and Seed Insects Working Party Conference (S2.07-01); 31 July-6 Aug. 1983; Athens, Georga, pp. 77-84.

Controlling Western Spruce Budworm in Spruce Seed Orchards in the Interior of British Columbia with Foliar Sprays

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Abstract

Sevin and Bacillus thuringiensis (B.t.) were applied operationally to protect a spruce seed orchard cone crop from western spruce budworm (Choristoneura occidentalis) in 1987. Sevin provided good protection to both cones and foliage. B.t. was not effective, however, multiple applications may have improved efficacy.

Introduction

Western spruce budworm (Choristoneura occidentalis Freeman)(WSB) is an important defoliator in the forests of western North America. Its hosts are Douglas-fir, the true firs, larch, spruce and occasionally pine and hemlock (Brookes, et al., 1985). Outbreaks of this insect are cyclic and extend over large areas. In 1986-1987, an infestation in the Kamloops Forest Region of British Columbia (B.C.) spread into the valley surrounding Skimikin Seed Orchards, (Fig. 1). Canadian Forestry Service surveys in 1986 predicted moderate to severe defoliation in 1987 (Wood and Van Sickle, 1986). This paper outlines the program to protect the cones in the seed orchard during the spring of 1987.

C. occidentalis overwinters as a second instar larvae (L2) in protected places on the tree. In the spring they emerge and disperse to feed. Feeding may begin with the larvae mining needles but when vegetative and reproductive buds begin to swell, the larvae burrow into them to feed. Damage continues as the foliage and cones expand. Epidemics can result in severe defoliation, reduced growth, deformity, dead tops and mortality (Unger, 1983). Damage to cones includes early abortion, tunneling and subsequent seed loss and case hardening due to excessive pitch flow and distortion following feeding.

The larvae grow through six instars (L1-L6) before pupating in late June or early July. Dispersal within a stand occurs during adult flight in July or August as well as in the spring when young larvae (L2-L3) are moved from tree to tree by air currents. Larval dispersal is largely finished by the time they have reached L3-L4.

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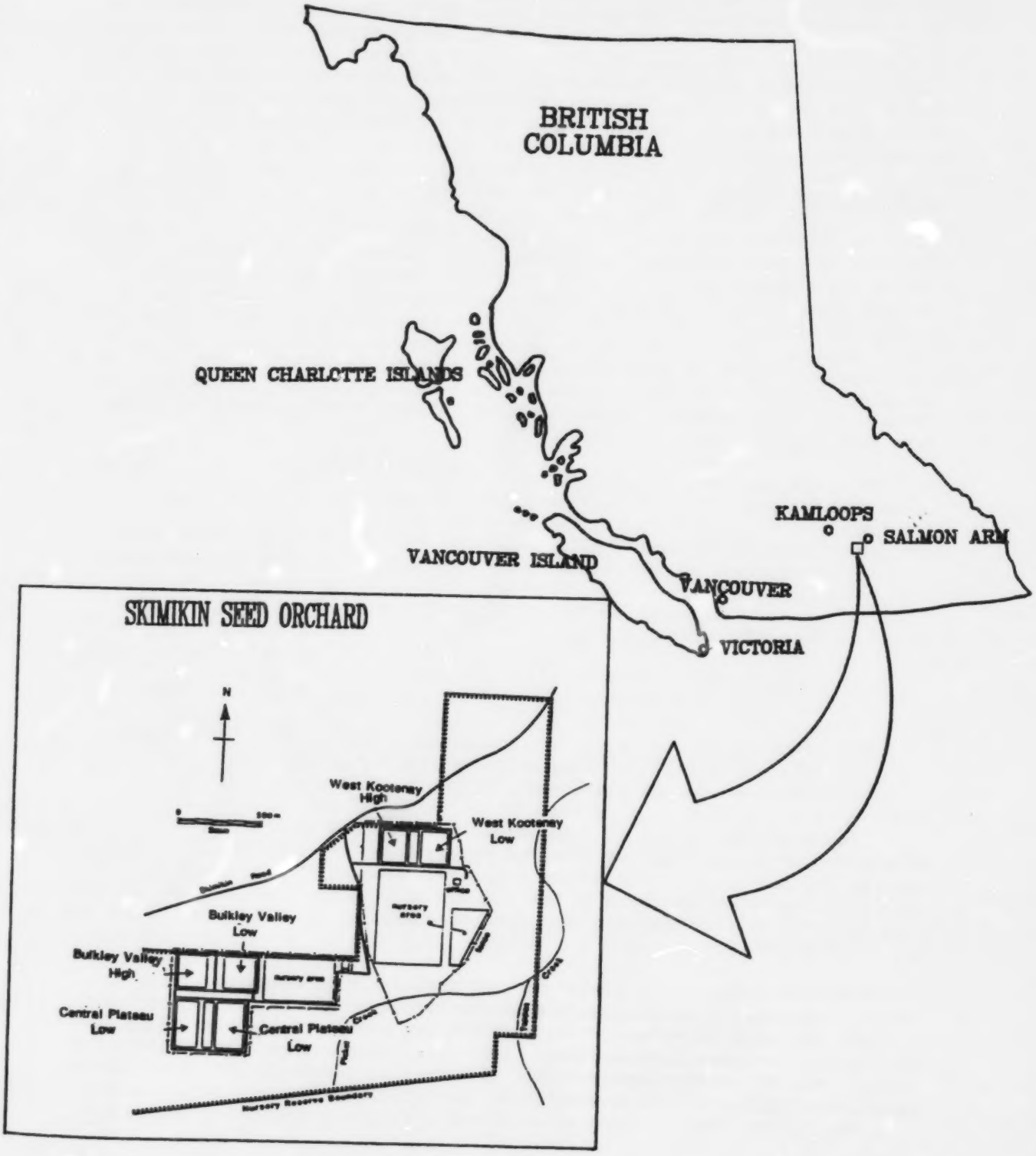
[1] Mention of trade names or products does not constitute an endorsement by the authors or the B.C. Ministry of Forests.

FIG. 1. SITE LOCATION AND ORGANIZATION AT SKIMIKIN SEED ORCHARD IN SALMON ARM, B.C., CANADA.



A great deal of effort has gone into managing WSB in forests and there are chemical and biological suppression methods available for use in high value Douglas-fir stands (Brookes, et al., 1985). The most common tactic is to apply an insecticide by air, in order to reduce defoliation caused by late instar feeding. Unfortunately most cone damage occurs earlier, when the young cones are elongating. Stipe and Hard (1980) and Stipe and Green (1981) showed that early spring insecticide applications could protect young Douglas-fir cones from damage. The purpose of our trial at Skimikin was to test insecticides operationally against WSB on spruce cones.

Materials and Methods

The Skimikin seed orchard complex is located near Salmon Arm, B.C. and is operated by the B.C. Ministry of Forests. It is composed of a grafted, clonal mix of white (Picea glauca (Moench) Voss) and engelmann (P. engelmannii Parry) spruce, planted at a five metre by five metre spacing. The orchard was planted in 1979-1980 but the trees vary from less than one metre to more than four metres tall because of roguing and replacement of lost trees. The facility is designed to produce seed for high and low elevations in three seed zones and is therefore divided into six seed orchards (Fig. 1): Central Plateau Low (CPL), and High (CPH), Bulkley Valley Low (BVL), and High (BVH), West Kootenay Low (WKL), and High (WKH).

The cone crop protection program at Skimikin consisted of the following early spray applications, between May 2 and 6, 1987:

(a) Sevin 50 WP (carbaryl), at 2.7 kg/1500 L water/ha applied to the entire BVH and BVL orchards using a Turbomist^{R} airblast sprayer. Kelthane (dicofol) (2 L/ha) was added as a preventative measure against outbreaks of the spruce spider mite (Oligonychus ununguis (Jacobi)).

(b) Sevin 50 WP (0.8 kg/500 L water) applied with a hydraulic sprayer to individual crop trees in the CPH and West Kootenay (WK) orchards.

(c) Bacillus thuringiensis Berliner, var. kurstaki (B.t.) (Thuricide HPC) at 21 BIU/1500 L water/ha applied to the entire CPL orchard using the Turbomist sprayer.

Treatments were timed to coincide with the period when WSB larvae were mainly second or third instar and were moving from overwintering sites into needles and new buds. Check blocks (areas not treated with an early spray) were comprised of those trees in the CPH and WK orchards that were not sprayed with Sevin as well as one edge (4-5 rows of trees) of the CPL orchard that was not treated with B.t.

Sampling methods were varied so that they could be compared in the future. Pre/post-spray assessments of the number of WSB in the WK and Central Plateau (CP) orchards were made by sampling 300 one year old twigs (3 twigs x 100 trees) throughout each orchard. Post spray samples from the treated crop trees in the WK and CPH orchards (51 - 57 trees per orchard) were made in the same manner (153 - 157 twigs sampled). In the Bulkley Valley (BV) orchards,

pre/post spray samples consisted of 300 one year old twigs (10 twigs x 30 trees) and 300 female buds (10 buds x 30 trees in each orchard). A similar female bud sample was made in the CPL, both before and after treatment. Sampling occurred on April 29 - 30 and again on May 16 - 17.

The entire seed orchard complex and adjacent windbreaks received an aerial spray of B.t. (Futura^{R}; 30 BIU/ha) on May 22, 1987. This was designed to prevent defoliation in untreated areas. Pre-aerial spray samples (May 18 - 19) were used to further assess the efficacy of the ground sprays. WSB populations were sampled by beating 45 centimetre branch tips (3 tips per tree x 30 trees per orchard) over a 0.54 m^2 beating tray and counting the live and dead budworms that were dislodged onto the tray.

Defoliation estimates and cone damage assessments were made in late June at which time adult moths were beginning to fly. Foliar damage was estimated visually at 25 percent increments on each of 39 - 41 trees per orchard (390 - 410 samples/orchard).

To estimate cone damage, the cones on 10 branches on each of 10 trees in each of the treatment areas were rated for WSB feeding. Ratings were 0, light, moderate, or heavy depending on the amount of damage.

Results and Discussion

The airblast applications of Sevin or B.t. initially reduced the number of WSB on twigs and cones substantially (Table 1; Table 2). The number of active larvae was reduced by an average of 94.2% between pre and post ground spray samples in May. Later samples also attest to the success of treatments. Pre-aerial spray branch beating data (Fig. 2) showed that the CPL (treated with a ground spray of B.t) and the BV orchards (treated with Sevin) had a much lower WSB population than the portions of the CPH or WK orchards that were not treated with an early spray.

Cone damage was also reduced (Fig. 3), however the ground spray of B.t. was not as effective as Sevin. This may have been due to the lack of residual activity with B.t. A second application of B.t., about a week after the first, may have been effective on late emerging larvae and/or larvae dispersing into the orchard from the surrounding windbreaks. Defoliation estimates (Fig. 4) indicate that the CPL had as much defoliation as areas of the CPH that did not receive an early spray. This also indicates that emergence or dispersal following the initial B.t. application contributed to the problem.

Under the conditions encountered in 1987 at Skimikin, an early spray of Sevin appears to be effective in reducing both cone damage and defoliation by WSB in spruce seed orchards. Stipe and Green (1981) found that two applications were required to protect Douglas-fir cones and no doubt if weather conditions had not been extremely good during our test, two applications of Sevin would probably have been required. B.t. was not efficacious in our test. While initial results were promising (Table 1) it appears that a long period of larval emergence and/or dispersal precludes success with a single application. Multiple applications of B.t. may be necessary to achieve acceptable levels of foliage and cone protection.

TABLE 1

AVERAGE NUMBER OF WESTERN SPRUCE BUDWORM (±S.E.) PER TWIG OR PER CONE IN SKIMIKIN SEED ORCHARDS SPRAYED WITH SEVIN 50 WP OR THURICIDE HPC USING A TURBOMIST AIRBLAST SPRAYER (1987).

		FOLIAGE ASSESSMENT		CONE ASSESSMENT	
ORCHARD	TREATMENT	PRE-TREATMENT	POST-TREATMENT	PRE-TREATMENT	POST-TREATMENT
CPL	THURICIDE	0.39 ± 0.06	0.04 ± 0.01	0.14 ± 0.02	0.03 ± 0.01
BVH	SEVIN	0.49 ± 0.04	0.02 ± 0.01	0.32 ± 0.04	0.01 ± 0.01
BVL	SEVIN	0.29 ± 0.03	0.01 ± 0.01	0.15 ± 0.03	0.003 ± 0.003

TABLE 2

AVERAGE NUMBER OF WESTERN SPRUCE BUDWORM (±S.E.) PER TWIG IN SKIMIKIN SEED ORCHARDS WHERE ONLY INDIVIDUAL CROP TREES WERE SPRAYED WITH SEVIN 50 WP USING A TRACTOR MOUNTED HYDRAULIC SPRAYER (1987).

ORCHARD	UNSPRAYED TREES	SPRAYED TREES
WKL	0.69 ± 0.05	0.06 ± 0.02
WKH	1.29 ± 0.07	0.05 ± 0.02
CPH	0.96 ± 0.09	0.05 ± 0.02

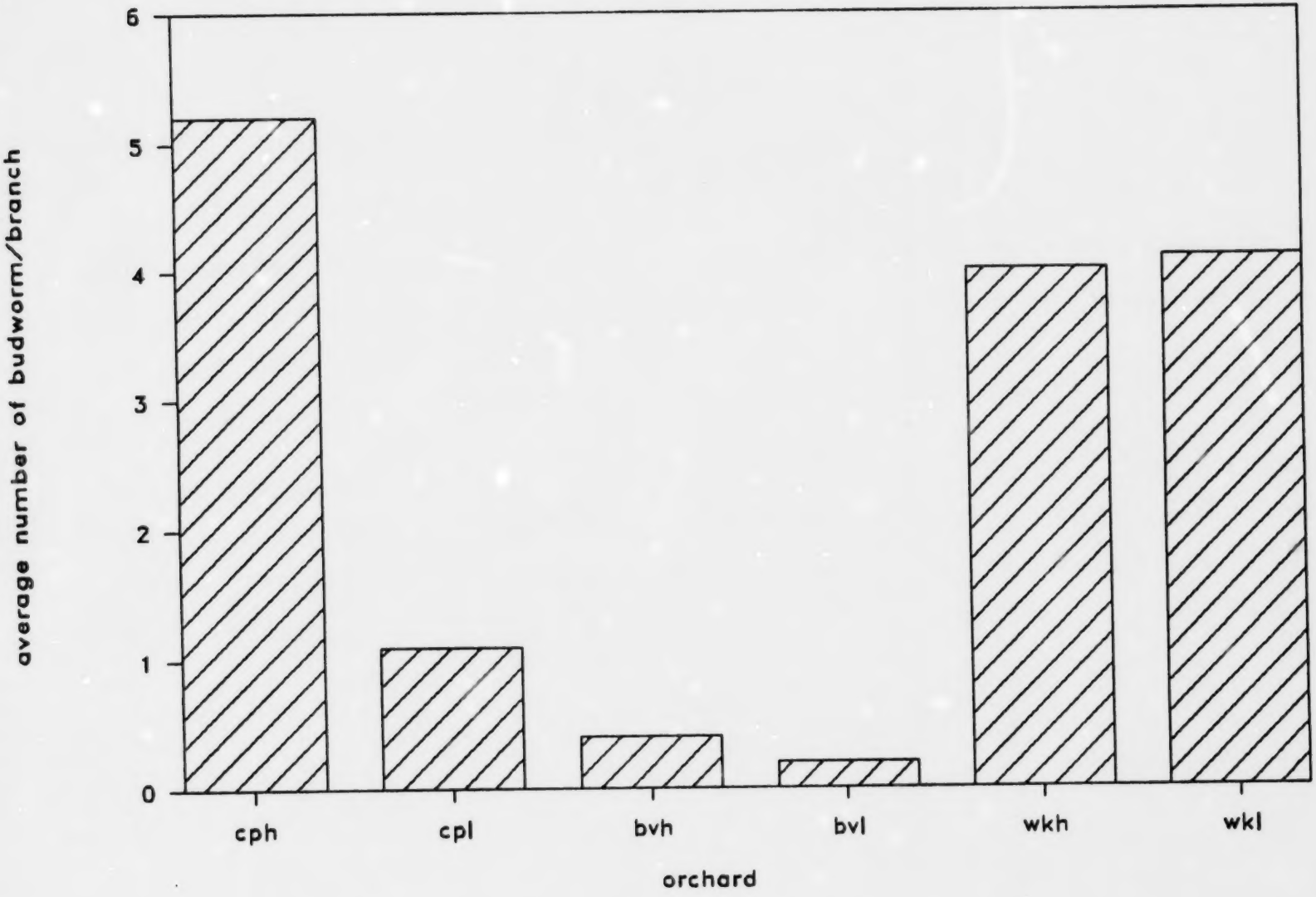


FIG. 2. AVERAGE NUMBER OF WESTERN SPRUCE BUDWORM PER BRANCH FOLLOWING GROUND SPRAY TREATMENTS AT SKIMIKIN SEED ORCHARDS

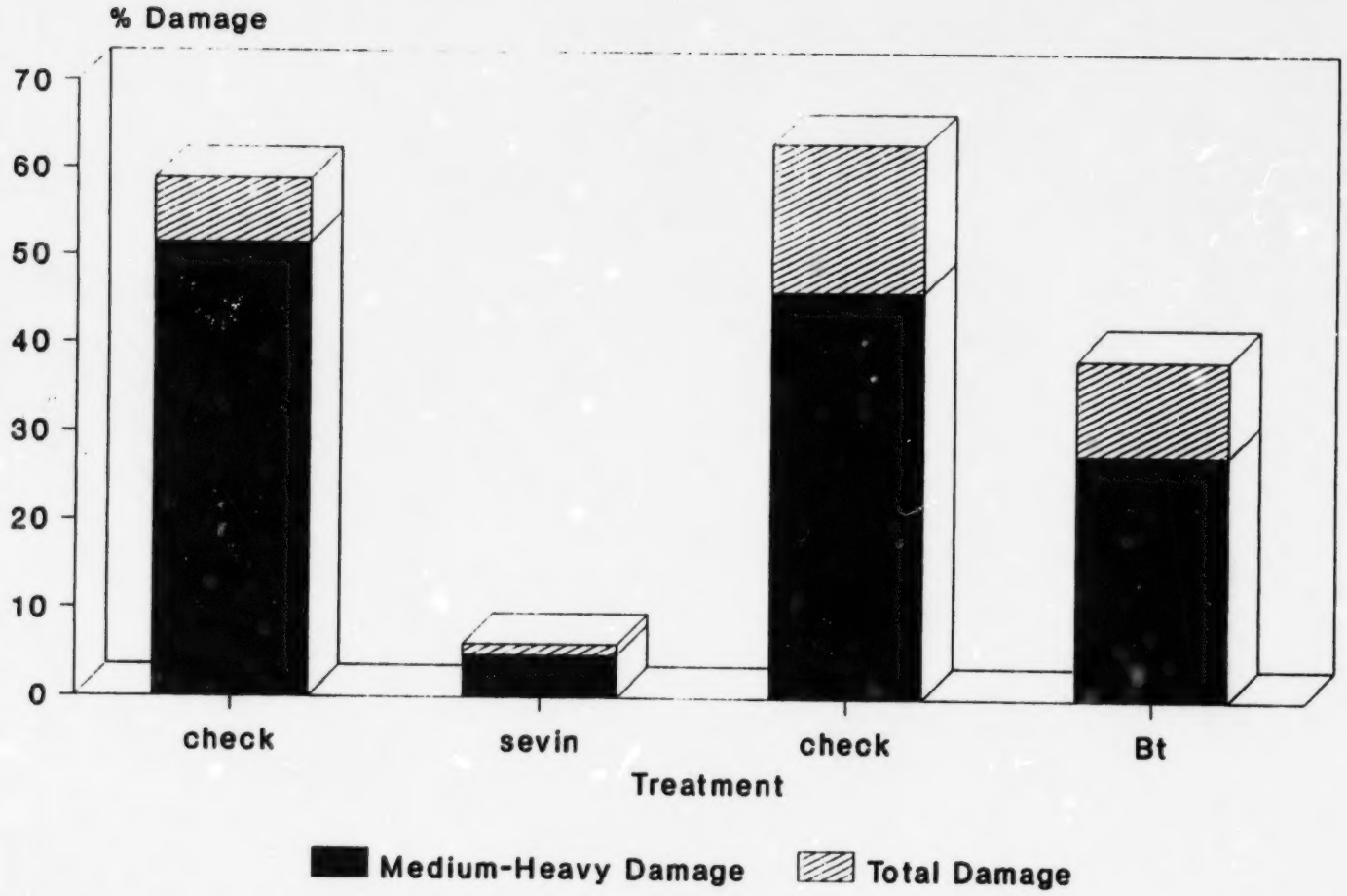


FIG. 3. PERCENT OF SPRUCE CONES DAMAGED BY WESTERN SPRUCE BUDWORM FOLLOWING SPRAY TREATMENTS AT SKIMIKIN SEED ORCHARDS IN 1987.

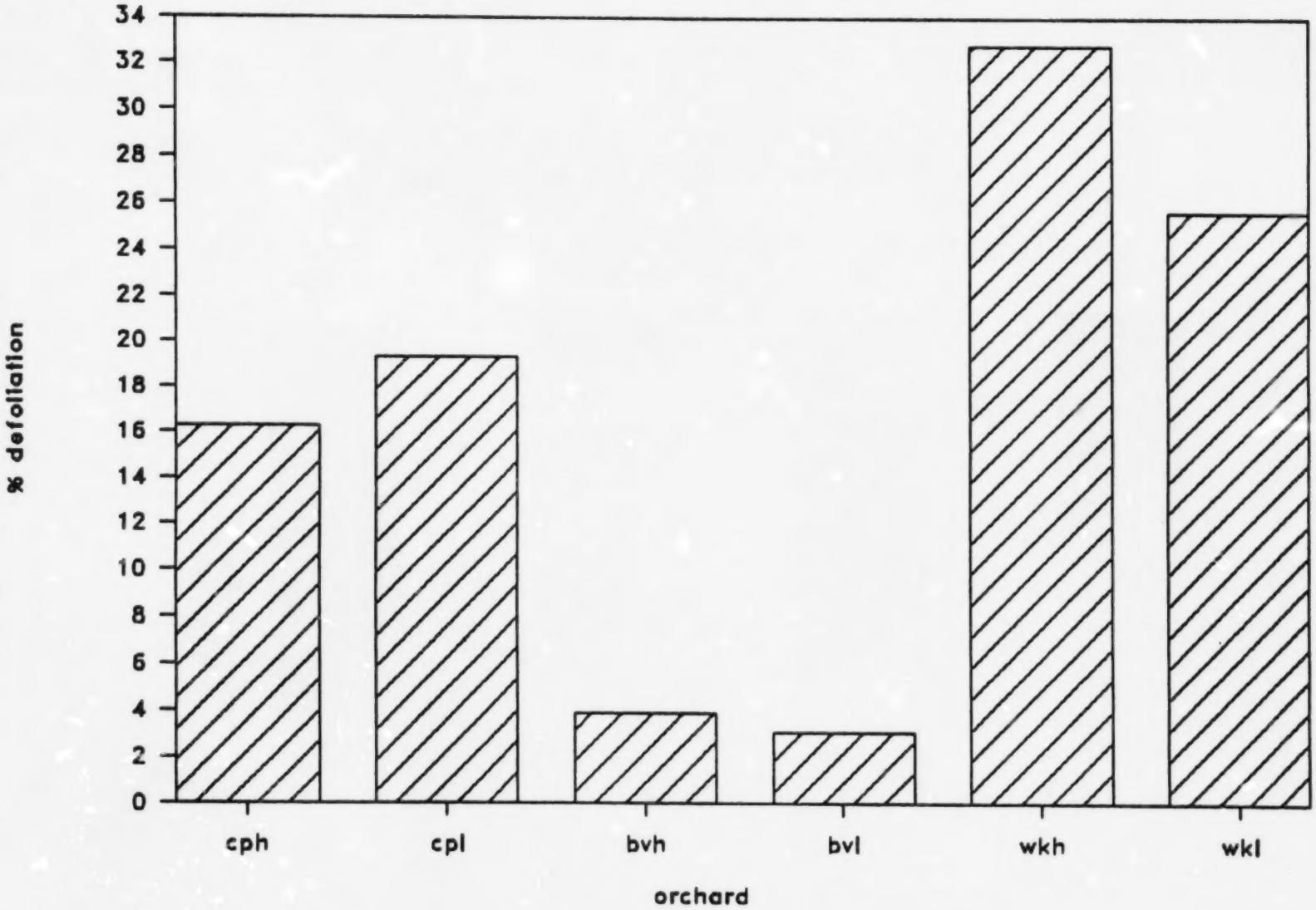


FIG. 4. DEFOLIATION ESTIMATES FOR ORCHARD TREES AT SKIMIKIN SEED ORCHARDS IN 1987 AFTER A CONTROL PROGRAM FOR WESTERN

Acknowledgements

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References Cited

Brookes, M.H., J.J. Colbert, R. G. Mitchell and R. W. Stark. 1985. Managing trees and stands susceptible to western spruce budworm. USDA-FS. Coop. State Res. Serv., Tech. Bull. No. 1695. 111 p.

Stipe, L.E. and J.S. Hard. 1980. An early single tree application for Douglas-fir foliage and cone protection from the western spruce budworm. Forest Insect and Disease Mgmt. USDA-FS Northern Region, Missoula Mont. Rept No. 80-3.

Stipe, L.E. and A.K. Green. 1981. A multiple ground application of acephate and carbaryl for protection of Douglas-fir cones from western spruce budworm. Forest Pest Management USDA-FS, CANUSA program Rept. 81-22.

Unger, L.S. 1983. Spruce budworms in British Columbia. Environ. Can. Can. For. Ser. Pest Leaflet 31 Victoria, B.C. 4 p.

Wood, C.S. and G. A. Van Sickle, 1986. Forest Insect and Disease Conditions - British Columbia and the Yukon, 1986. Can. For. Serv. Pacific For. Centre, Victoria, B.C.-X-287.

Spring and Fall Trunk-Implanted Acephate for Protection of Douglas-fir from Defoliation by the Western Spruce Budworm [1/,2/]

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ABSTRACT

April or November treatments of trunk implanted acephate were more effective than May treatments to protect superior Douglas-fir (Pseudotsuga menziesii var. glauca) from defoliation by western spruce budworm (Choristoneura occidentalis) and spruce coneworm (Dioryctria reniculelloides).

INTRODUCTION

Western spruce budworm (Choristoneura occidentalis Freeman) and spruce coneworm (Dioryctria reniculelloides Mutuura and Monroe) are well-known defoliators of true fir (Abies spp.) and Douglas-fir (Pseudotsuga menziesii) forests, and destroyers of Douglas-fir cone crops (Dewey 1970, Dewey 1986, Chrisman et al. 1983). Consumption of foliage by the larvae damages or kills new shoot growth, reducing both leaf biomass and production of seed cones. Repeated destruction of new foliage may also deplete nutrient reserves in trees, rendering them unable to produce cone crops in future years.

In previously reported studies, acephate insecticide, implanted in the boles of trees, protected foliage of grand fir (Abies grandis) from defoliation by western spruce budworm (Reardon and Haskett 1981, Reardon and Barrett 1984). Acephate implanted in Douglas-fir also reduced damage by the budworm and resulted in increased seed yields (Reardon et al. 1985, Stipe and Dewey 1985, Thier 1986). We were impressed with the apparent effectiveness of the acephate implants, but we were concerned whether the method could be implemented when road and weather conditions are favorable for efficient field operations. We therefore conducted these experiments to compare effectiveness of spring and fall treatments.

1/ This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

2/ Mention of proprietary products is for identification only and does not imply endorsement of these products by the U.S. Department of Agriculture.

MATERIALS AND METHODS

Experiment 1--Capsules, containing 0.875 g of acephate insecticide were implanted in holes drilled into the sapwood of Douglas-firs every 10 cm around the tree bole, 1 m above ground. Acephate capsules marketed and registered for this use pattern are available under the trade name Acecap 97 (E.P.A. Reg. #37979-1, Creative Sales Inc., Fremont, NE 86025).

We applied treatments in April and May 1985 on the Umatilla National Forest, Oregon. Twenty of the 60 selected trees were randomly chosen to be treated April 24, about 3 weeks before cone buds opened. A second set of 20 trees was treated May 13. The third set of 20 trees was an untreated control.

Experiment 2--Similar treatments were applied in late fall and early spring to widely separated superior Douglas-firs on the Wallowa-Whitman National Forest, Oregon. Forty-five trees were selected and 15 randomly assigned to each of 2 treatment times: Oct 29-Nov 8, 1985; March 25-Apr 4, 1986. The remaining trees were untreated controls.

In 1985, we randomly chose 10 trees from each treatment to assess amount of defoliation and insect population levels. In 1986 a similar procedure was followed to estimate defoliation from each of 15 trees in each treatment (Koerber and Sandquist 1988).

RESULTS

Treatment with acephate in either early spring or late fall was more effective than treatment in late spring. Both insecticide treatments applied in 1985 (April and May were the early and late treatments in Fig. 1) greatly reduced the proportion of shoots in the 100% defoliation class and increased the proportion found in lower defoliation classes. Trees receiving early implants had 52% of new shoots with no defoliation and 75% in the less than 26% defoliated classes. Trees receiving later implants had 25% of new shoots with no defoliation and 46% in the less than 26% defoliated classes. Samples from untreated trees showed 90% of new shoots completely defoliated and less than 5% in the less than 76% defoliated classes. Both April and May treatments differed significantly from the untreated controls (χ^2 = 2727 and 641, respectively, P <0.01). The early and late treatments were not significantly different from each other (χ^2 =0.21).

These relationships were confirmed by data on the oven-dry weight of surviving foliage. The control differed significantly from the two acephate treatments and the two acephate treatments from each other, the April treatment having more biomass. Data on the number of surviving buds and surviving insect population density showed a positive treatment effect compared to the untreated trees. The differences between the two treatments were insignificant (Koerber and Sandquist 1988).

In the second study, both fall and spring acephate treatments greatly reduced defoliation (Fig. 2). No samples from any of the treated trees fell into the 100% defoliation class and most were in the no defoliation class, while 77% of untreated samples were in the more than 76% defoliation classes. The fall and spring treatments were virtually identical in effectiveness and both were significantly different from the controls (χ^2 = 18.08 and 18.43, respectively, P <0.01).

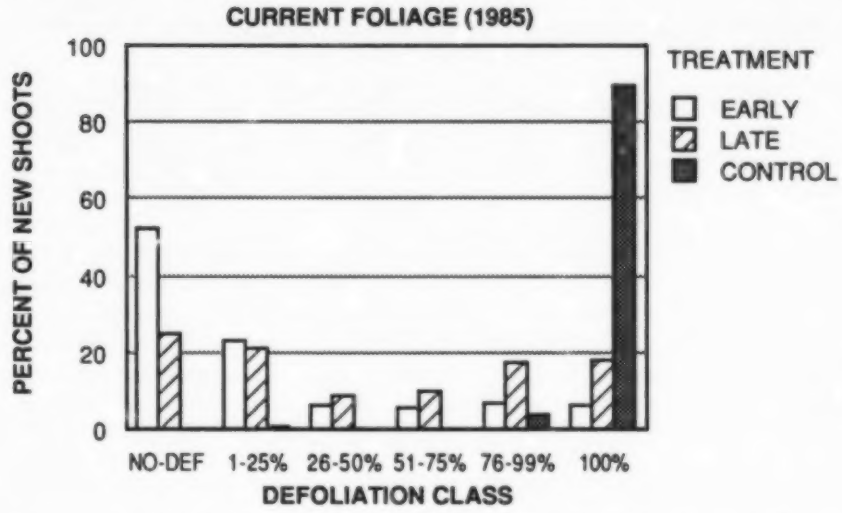

Figure 1. Defoliation of 1985 Douglas-fir shoot growth in relation to date of acephate implant treatment.

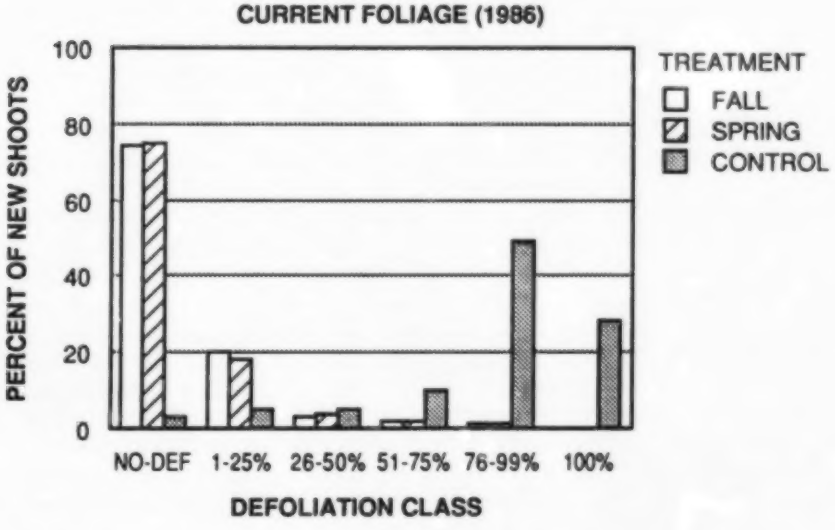

Figure 2. Defoliation of 1986 Douglas-fir shoot growth in relation to date of acephate implant treatment.

DISCUSSION

Data from defoliation estimates were well supported by foliage dry weight measurements in the 1985 study. In both 1985 and 1986 the difference in foliage complement between treated and untreated trees was obvious from distances up to 1000m to even the most casual observers. We confirmed our observations of defoliation by classifying branch samples by proportion of shoots defoliated. Our data on bud production showed that trees treated in April and May produced 4.5 and 4.9 times as many buds as untreated trees. The reduction in live bud complement on untreated trees indicates that the effects of defoliation or the benefits of acephate treatment carry over into the next growing season.

The equal effectiveness of spring and fall treatments for foliage protection suggests that implanted acephate is not metabolized by the trees during the winter months and concentrations toxic to the target insect larvae are present in the new foliage in the spring.

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LITERATURE CITED

Chrisman, A. C., G. M. Blake, and R. C. Shearer. 1983. Effect of western spruce budworm on Douglas-fir cone production in western Montana. USDA For. Serv. Res. Pap. INT-308. 7 p.

Dewey, J. E. 1970. Damage to Douglas-fir cones by Choristoneura occidentalis. J. Econ. Entomol. 63:1804-1806.

Dewey, J. E. 1986. Western spruce budworm impact on Douglas-fir cone production. p. 243-245 in Conifer tree seed in the Inland Mountain West, Symp. Proc. USDA For. Serv. Tech. Rep. INT-203.

Koerber, T. W. and R. E. Sandquist. 1988. Timing of trunk-implanted acephate for protection of Douglas-fir from defoliation by the western spruce budworm. Western J. of Appl. For. (in press).

Reardon, R. C. and M. J. Haskett. 1981. Effect of orthene medicaps on populations of western spruce budworm on grand fir and Douglas-fir. J. Econ. Entomol. 74:266-270.

Reardon, R. C. and L. Barrett. 1984. Effects of treating western spruce budworm populations on grand fir and Douglas-fir with acephate, carbofuran, dimethoate, oxydemetonmethyl, and methamidophos. For. Ecol. Manage. 8:1-10.

Reardon, R. C., L. J. Barrett, T. W. Koerber, L. E. Stipe, and J. E. Dewey. 1985. Implantation and injection of systemics to suppress seed and cone insects in Douglas-fir in Montana. Can. Entomol. 117:961-969.

Stipe, L. E. and J. E. Dewey. 1985. Protecting Douglas-fir cones and foliage with a systemic insecticide. USDA For. Serv. Rep. 85-6., Missoula, MT. 21 p.

Thier, R. W. 1986. Operational use of systemic insecticide implants to suppress western spruce budworm in Douglas-fir cones in Idaho. USDA For. Serv. Rep. 86-4., Ogden, UT. 8 p.

INJECTION OF INSECTICIDES INTO NORWAY SPRUCE (PICEA ABIES KARST.) TRUNK TO PROTECT SEED YIELD FROM INSECTS

by

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SUMMARY

In Lithuania seed orchards of Norway spruce (Picea abies Karst.) cover an area of over 350 ha. In good years some of them yield 20 kg per ha spruce cones. Cone and seed insects cause seed losses up to 15-40% every year. Application of insecticides for seed protection is always hazardous to the surroundings. Injections of insecticides may cause the least possible damage to the environment.

In a spruce seed orchard (at Dubrava FES, central Lithuania) three insecticides have been tested by way of injections: cimbush (Cypermetrin) - a contact insecticide, antio (Fomothion) - a systemic-contact insecticide and BI-58 (Dimethoate, Rogor, Phosphamide) - a systemic insecticide. In the middle of May trees received trunk-injections of insecticides (2,5% a.i.) of self-run-in. The dose contained 0,2 g (a.i.) of an insecticide per 1 cm of tree diameter. On the whole, producing trees received 200 g of an insecticide (2,5% a.i.).

Having made a detailed analysis of cones in autumn, it has been ascertained that the most effective for seed crop protection were the BI-58 insecticide injections. After this treatment seed damage by the conobiont-phytophagan populations has been reduced by 65%, while the absolute insect-damage (D_a) was 2,6 times less than in the control variant. The total number of damaged cones after the BI-58 insecticide application was reduced by 51%. Antio was less effective. Nevertheless, in this treatment 42% of seeds were protected, while the seed damage reduced by 30%. The least effective was the contact insecticide cimbush. In this treatment the significance of the total number of damaged cones against the control was $p<0,05$. Nevertheless, cimbush has protected 23% of seed yield ($p>0,05$). In all the treatments three species of insects appeared to be the most harmful: Cydia strobilella L., Dioryctria abietella Den. et Schiff. and Lasiomma anthracinum Czerny. The germination power of spruce seeds was high (>85%).

Keywords: insecticide, injection, seed protection, conobiont-phytophagan populations.

INTRODUCTION

Spruce stands in Lithuania make up 20,7% of the total area occupied by forests. In 1964 the work of growing up a permanent seed bank of Norway spruce (Picea abies Karst.) for future high quality seeding material was

begun. At present there are over 350 ha of seed orchards of the species in our republic. In productive years some seed orchards yield up to 20 kg/ha spruce seeds. Nevertheless, we have found out that seed losses in these orchards reach about 15-40% yearly due to insect-damage, while in natural spruce stands they make up 60%. Thus, seed protection is one of the most important tasks in forest protection today. Practically, chemical way of seed yield protection is the most effective and widely-spread. But the use of chemical materials always causes contamination of the environment. Thus, methods of chemical protection reducing negative pesticide activity are being worked out in our country. For this purpose we have studied another method of seed protection - the masking method (Dumcius 1985; 1986). Under the conditions of seed orchards or parks such a task may be well solved by preparation-injections which make the plant tissue unsuitable for pest development. Besides, injections may be applied even in bad weather, including wind and rain, greatly affecting spraying.

Practically several ways of insecticide introduction in vitro are known:

1. Spraying (the preparation penetrates through the cuticle, and also through the young bark of shoots).

2. Insecticide application through soil (the roots of a plant absorb the preparation).

3. Lubrication (the preparation is spread over free from bark places and penetrates through the bark remains and cambium).

4. Application through the sections of cut branches (the preparation is absorbed by a tree directly through cross-sections).

5. Trunk-injections of liquid preparations (the preparation is introduced into the xylem of a tree under pressure or without it).

When chemicals are used for protection of separate objects, then injections are most perspective. In the scientific literature this method of protection is known under the old name - the method of interior therapy or intraplant method. In the Soviet Union abundant investigations on injection application to protect seed yield of various tree species were carried out by A.N. Smetanin (1976, 1977). He tested trunk-injections of the Rogor emulsion to various coniferous trees by using injectors of special construction. The author admits that for spruce, fir and pine the dose of concentrated Rogor emulsion in May-June must not exceed 5 g per 1 cm trunk diameter, while later on greater quantities may be applied (Smetanin, 1977). However, the author does not point out the age and height of trees treated with such a dosing.

Other authors received good results by applying BI-58 injections to spruce and larch trees (Naumov, Bortnik, Stadnitskiy, 1976). It was noted that after application of 2-4 ml per 1 cm of spruce trunk about 66-100% of the larvae of Pegohylemia anthracina Czerny and the caterpillars of Laspeyresia strobilella L. are killed on the third day, while on the 5-7th day all the harmful insects are killed. In such a way seed protection is ensured by 80-90%.

The method of injections has been widely studied by American and Canadian scientists. Solutions were trunk-injected through drilled holes by various injectors (Merkel, 1970; Merkel, De Barr, 1971; Helburg, Schomaker, Morrow, 1973; Filer, 1973; Reardon et al., 1983, 1985; Fogal, Lopushanski, 1983; Koerber, Merkin, 1983; Summers, Miller, 1986).

For cone and seed protection in the United States trunk-injections of dimethoate, oxydemeton-methyl and dicrotophos were applied to seed producing trees of slash pine (Pinus ellioti Engelm.) (Merkel, 1970). Insecticides were applied at the rate of 5 g per every 2,5 cm of trunk diameter. Using the dose of 5 g the populations of Dioryctria sp. and Laspeyresia sp. were killed by 80-97%.

Good results showed the application of dicrotophos (Bidrin) to slash pine (P. ellioti Engelm.) trunks in the North Florida (Merkel, De Barr, 1971). Dicrotophos was applied with an injector at the rate of 0,6-1,4 g (a.i.) per 1 cm of trunk diameter and into bore-holes 1,3 cm in diameter to a depth of 7,6 cm with a syringe at the rate of 0,8-2 g/cm. The results of cone analysis have shown that the most effective was the introduction of insecticides into bore-holes. In this treatment cone infestation by pests was reduced by 88-100%. Infestation of trees treated with an injector was reduced by 30-97%.

Two ways of injections were used for Douglas-fir (Pseudotsuga menziesii Franco) seed crop protection in the United States: trunk-injections of oxydemeton-methyl and acephate into trees with Mauget injector, and implantation of dimethoate and acephate into trees by special plastic cartridges (1x3 cm) (Reardon et al., 1983, 1985). Each "syringe" with oxydemeton-methyl (50% of MetaSystox-R) contained 1,5 g (a.i.), while with acephate (Orthene) - 1,8 g (a.i.). Implantation of insecticides was performed by inserting gelatin capsules with dry preparation into drilled in a tree holes where it dissolved from the sap together with it's capsule. Every capsule with acephate contained 0,9 g (a.i.), with dimethoate - 0,6 g (a.i.).

Experiments have shown that all the methods of application, except dimethoate implantation, have significantly increased the number of filled seeds per cone. It was noted that acephate was the most effective against the caterpillars of Choristoneura occidentalis Freeman and Dioryctria reniculelloides Muntuura-Munroe.

Good results after trunk-injections of the systemic insecticide MetaSystox-R to Douglas-fir trees were obtained also by other investigators (Koerber, Merkin, 1983). Experiments have been conducted in Oregon, California and Washington (USA). Seed yield after insecticide-injections at the rate of 1,5 per every 15 cm of tree circumference increased up to 245%. It was admitted that the residues of MetaSystox-R in cones and leaves of separate trees distributed unevenly.

In Canada (British Columbia) there were performed experiments with injections of systemic insecticides and foliar sprays to Douglas-fir trees to protect seed yield against harmful insects (Summers, Miller, 1986). Injectors used contained 3 ml of 50% (a.i.) oxydemeton-methyl and 5 ml of 35% (a.i.) acephate. Experiments have shown that the injections of oxydemeton-methyl were less effective than foliar sprays in controlling insect damage, but acephate injections gave poor results. There is some data on dicrotophos

(doses of 0,56 and 1,12 g (a.i.) per 1 cm of trunk diameter) and oxydemeton-methyl (doses of 0,36 and 0,72 g a.i./cm) application to white-spruce (Picea glauca Voss.) trees (Fogal, Lopushanski, 1983). The experiments were conducted in Ontario, Canada. Insecticides were introduced into drilled holes at the stumps of trees with Mauget injectors. The authors admitted almost complete absence of cone attacks by various conobiont-phytophagan species in the year of treatments. Besides, it has been ascertained that in some cases when the application rate was 1,12 g a.i./cm dicrotophos revealed phytotoxicity.

MATERIALS AND METHODS

Seed yield protection of Norway spruce was carried out by trunk injections of liquid preparations into standing trees. The investigations took place at a seed orchard of Dubrava FES (central Lithuania, Kaunas region). Selected experimental trees had almost the same taxational characteristics (Table 1). Efficacy tests of the method against harmful conobionts were performed by analysing differences in their activity insecticides: cimbush, 25% e.c. (Cypermetrin) - a contact insecticide, antio, 25% e.c. (Formothion) - a contact-systemic insecticide and BI-58, 40% e.c. (Dimethoate, Rogor, Phosphamide) - a systemic insecticide. Each insecticide was applied as water emulsion at 2,5% concentration (a.i. = active ingredient) with 5 replications. The total rate of each trunk-injected insecticide (2,5% a.i.) was 200 g on the account that the dose per 1 cm of trunk diameter was 0,2 g a.i. Insecticide injections began at the moment of full opening of female buds (05.11) and continued till the beginning of conelets' turning down (05.15). Mean temperature during the period was +14°C, while relative air humidity - 66-88%. Mean precipitation quantity did not exceed 1 mm.

Insecticides were injected at the stump of trees 15-20 cm above the ground. Holes (1 cm in diameter) were drilled with a boring machine into the xylem of a tree. The holes were directed downwards at an angle of 45° from three sides at 25-29 cm intervals around the circumference of a tree trunk to a depth of 2-2,5 cm beyond the inner bark. Glass tubes of the same diameter with 14 cm^3 capacity were placed into the drilled holes. The outside of the glass tubes was hermeticized with the tree bark by plasticine. In such a way insecticides together with the sap went upwards into the crown. Insecticide consumption at a time was 40 g per tree. Consequent re-filling of the glass tubes was done after complete absorption of the previous dose.

After implantation of the required dose of an insecticide the glass tubes were removed. Then the holes were closely plugged up with pine sap stoppers to escape evaporation and dropping of pests and fungi spores. The observations of cone development stages in crowns of experimental trees were performed with field glasses once a week during the whole vegetative season. Female buds damaged by insects were collected soon after detection. All the remaining cones from each experimental tree were collected in October at harvest. A detailed analysis of cones was done according to G.V. Stadnitskiy et al. (1978) methodics. Based on the data, relative and absolute cone damages by separate pest species were determined by the formulae:

Table 1. Taxational characteristics of experimental trees, application rate and absorption of injected insecticides

Treatment	Concentration of an insecticide a.i., %	Taxational characteristics of experimental trees		Rate per tree, g	Daily absorption by a tree, g	Rate per 1 cm of trunk diameter, g	
		Height, m	Stem diameter, cm (at the height of 1,3 m)			According to a.i. $\bar{X} \pm SD$	According to the preparation $\bar{X} \pm SD$
Antio, 25% e.c.	2,5	13,8±0,4	23,4±0,7	200	40	0,2±0,01	0,9±0,03
Cimbush, 25% e.c.	2,5	13,6±0,2	22,1±0,6	200	40	0,2±0,01	0,9±0,02
BI-58, 40% e.c. (standard)	2,5	13,4±0,2	24,9±0,5	200	40	0,2±0,01	0,5±0,01
Control	-	12,6±0,5	21,6±0,7	-	-	-	-

$$D_r = \frac{M_1 \cdot 100}{M}, \ (\%)$$

where D_r - relative cone damage by a pest species;

M_1 - number of cones damaged by the given pest, units;

M - total number of cones in a variant, units;

$$D_a = \frac{A}{M}, \ (\text{spec./cone})$$

where D_a - absolute cone damage by a pest species;

A - total number of specimens of the given pest (larvae, caterpillars, puparia or damage signs) found in cones.

Seed losses (L) due to each pest species were defined by the formula:

$$L = \frac{D_r \cdot K}{100}, \ (\%)$$

where K - mean seed loss per cone damaged by the given pest, %.

Separately defined is the loss of seeds due to both the species of seminiphagous insects (Megastigmus abietis Seitn. and Plemeliella abietina Seitn.). For this purpose all the gathered cones from each experimental tree separately were dried in a thermostat (2V-151) at the temperature of 30-35°C. From the extracted amount of seeds 500 of them from each tree were taken and dissected. The resulting summarized seed loss (ΣL) due to the harmful entomocomplex was determined. Methods of mathematical statistics were used to analyse the data. The significance of difference between treatments was analysed according to the Student's test. Seed germination was defined for each treatment separately.

RESULTS AND DISCUSSION

In our experiments seed yield protection of Norway spruce (Picea abies Karst.) against harmful conobionts was conducted by way of trunk-injections (to growing trees) of three different in their activity insecticides: antio, 25% e.c., cimbush, 25% e.c. and BI-58, 40% e.c. Treated 20-year-old trees were 13-14 m in height and trunk diameter averaged 22-25 cm (Table 1). Insecticides were introduced into the xylem at the stump by self-run-in without additional pressure. The average air temperature was 14°C (11,8-16,5) and relative air humidity - 66-88%, each spruce-tree absorbed 40 g of an insecticide (2,5% a.i.) per day. In all the treatments average rate of insecticide application per 1 cm of tree diameter was 0,2 g (a.i.).

As the treatments have shown, the best results were achieved with the BI-58 systemic insecticide. Mean number of damaged cones here decreased twice and did not exceed 31% on an average with the significance of difference in

comparison with the control being p>0,05 (Table 2). In this treatment the absolute cone damage (D_a) by harmful conobiont species was 0,8 units/cone, while in the control variant - 2,1 units/cone. It means that in the treatment the absolute number of vital specimens of all species reduced by 2,6 times (Table 3). Besides, female buds were not destroyed by Dioryctria shuetzeela (Fuchs.) and Ernobius tabidus Ksw. BI-58 injections were most effective against Cydia strobilella (L.), Dioryctria abietella (Den. et Schiff.) and Lasiomma anthracinum (Czerny.). Experiments have shown that cone damage by these pests reduced by 1,9, 2,6 and 3,9 times respectively (Table 3). Nevertheless, in this variant the caterpillars of C. strobilella (L.) and D. abietella (Den. et Schiff.) damaged 15,7 and 13,2% of cones respectively. After the BI-58 insecticide application the absolute cone damage (D_a) by these pests was reduced by 2 and 4 times respectively (Table 3). Cone damage by Kaltenbachiola strobi (Winn.) and Eupithecia sp. was reduced by 45 and 54% respectively.

The mean summarized seed loss from all the entomocomplex was 14,4 ± 0,4% with the significance of difference as compared with the control being p>0,05 and the coefficient of variation - 5,6% (Table 2). As can be seen, injections of the insecticide reduced seed losses by 65%. The greatest damage here was done by the caterpillars of C. strobilella (L.) and D. abietella (Den. et Schiff.). Both the species damaged about 60% of seeds from the total number in this treatment (Table 4). However, trials have shown that when BI-58 has been applied the damage by the two pests as compared with the control was reduced more than by 55% (Table 4).

Among all the species of cone and seed pests the BI-58 insecticide turned to be the most effective against L. anthracinum (Czerny.). The absolute spruce cone damage by the pest was reduced 3 times what contributed to damage reduction by 76% (Tables 3 and 4). It is necessary to admit that after BI-58 application seed loss from both seminiphagous insects (Megastigmus abietis Seitn. and Plemeliella abietina Seitn.) was reduced by 55% (Table 5). Seed damage by Plemeliella abietina (Seitn.) here was reduced by 13 times.

Injections of the systemic-contact insecticide antio were less effective. As compared with the BI-58 treatment seed damage was greater by 43% (Table 2). However, in comparison with the control seed damage by all the entomocomplex was reduced by 30% with the significance of difference being p>0,05 and the coefficient of variation - 12,2%. We must note that in this treatment female buds though not abundant but were already damaged by D. schuetzeela (Fuchs.) and E. tabidus (Ksw.) by 2,1 and 0,1% respectively (Table 3). Treatments have shown that injections of antio at the rate of 0,22 g (a.i.) per 1 cm of trunk diameter could not protect female buds from damage by D. schuetzeella (Fuchs.). Nevertheless, reduction of damage to female buds by E. tabidus Ksw.) was sufficient.

Like BI-58, antio was applied to trees where most of cones were damaged by two pests: C. strobilella (L.) and D. abietella (Den. et Schiff.) - averaging 22% by each of the species (Table 3). As compared with the control, injections of antio reduced cone damage by C. strobilella (L.) and D. abietella (Den. et Schiff.) by 27 and 36% respectively. The most effective injections of antio were against L. anthracinum (Czerny.). The average number of cones damaged by the pest reduced approximately by 2,5 times (Table 3).

Table 2. Insecticide-injection efficacy against spruce cone and seed pests

Treatment	% cones/seeds attacked		Statistical significance, %		Difference as compared with the Control		Difference as compared with the Standard	
	$\bar{X}$	SD	CV	P	%	P	%	P
Antio, 25% e.c.	44,1 23,8	2,4 1,-	12,2 9,8	5,4 4,4	69,8 57,6	>0,05 >0,05	143,2 165,3	>0,05 >0,05
Cimbush, 25% e.c.	56,2 31,7	2,5 1,3	9,9 8,9	4,5 4,-	88,9 76,7	<0,05 >0,05	182,5 220,1	>0,05 >0,05
BI-58, 40% e.c. (standard)	30,8 14,4	1,6 0,4	11,6 5,6	5,1 2,5	48,7 34,9	>0,05 >0,05	100,- 100,-	- -
Control	63,2 41,3	3,3 1,9	11,6 10,2	5,2 4,6	100,- 100,-	- -	- -	- -

Symbols: $\bar{X}$ - mean;
SD - standard deviation;
CV - coefficient of variation;
P - experiment precision;
p - significance of difference (according to the Student's test).

Table 3. Relative (D_r) and absolute (D_a) spruce cone damages by pests after insecticide injections

Treatment	Number of cones	D_r (%)/D_a (spec./cone)							Total insect damage, % ED_a
		Dioryctria schuetzeella	Ernobius tabidus	Cydia strobilella	Dioryctria abietella	Eupithecia sp.	Kaltenbachiola strobi	Lasiomma anthracinum	
Antio, 25% e.c.	403	2,1 / <0,1	0,1 / <0,1	22,2 / 0,3	21,9 / 0,3	2,4 / <0,1	5,- / 0,4	7,9 / 0,1	44,1 / 1,2
Cimbush, 25% e.c.	231	0,3 / <0,1	1,9 / <0,1	25,9 / 0,5	32,9 / 0,4	4,9 / 0,1	7,4 / 0,6	13,6 / 0,1	56,2 / 1,7
BI-58 40% e.c. (standard)	369	-	-	15,7 / 0,3	13,2 / 0,1	2,5 / <0,1	4,6 / 0,3	5,- / 0,1	30,8 / 0,8
Control	244	1,8 / <0,1	1,6 / <0,1	30,3 / 0,6	34,4 / 0,4	5,5 / 0,1	8,4 / 0,7	19,5 / 0,3	63,2 / 2,1

Cone damage by K. strobi (Winn.) was similar to that in the treatment with BI-58.

The summarized seed damage by all insects did not exceed 24% on an average (Table 2). In comparison with the control seed loss here was reduced by more than 40% with the significance of difference being $p>0,05$ and the coefficient of variation - 9,8%. But as compared with BI-58, seed loss in the treatment with antio increased by 65% (Table 2). The cause of it is that after the application of antio the absolute cone damage (D_a) increased by 1,5 times more than in the treatment with BI-58, and this has influenced by increase in damage by insects (Table 3).

The greatest damage to seeds in this treatment was done by the caterpillars of C. strobilella (L.) and D. abietella (Den. et Schiff.). They have damaged 60% from the total amount of damaged seeds (Table 4). Though as compared with the control, seed damage by C. strobilella (L.) was reduced by 30%, while by D. abietella (Den. et Schiff.) - by 26%. Besides, seed damage by L. anthracinum (Czerny.) after antio application was reduced by 60%. Injections of antio were effective against seminiphagous insects (M. abietis Seitn. and P. abietina Seitn.), since seed damage done by them was reduced by 2,5 times (Table 5).

Spruce yield protection was least effective in treatments with the contact insecticide cimbush. Seed damage was reduced only by 11% (Table 2). As compared with the standard (BI-58), total number of cones damaged by insects in this treatment was greater by approximately 83% with the significance of difference being $p>0,05$.

Better results were obtained after cimbush application in order to reduce the damage done by the caterpillar of D. schuetzeela (Fuchs.) and the larvae of L. anthracinum (Czerny.). In comparison with the control damage to female buds by the caterpillars of D. schuetzeela (Fuchs.) was reduced by 83%, while cone damage by L. anthracinum (Czerny.) - by 30% (Table 3). In this case the absolute cone damage (D_a) by the larvae of L. anthracinum (Czerny.) was reduced by 3 times and this preconditioned reduction in seed losses due to the pest by approximately 38% (Tables 3 and 4).

Injections of cimbush against E. tabidus (Ksw.) and D. abietella (Den. et Schiff.) were not effective. Seed damage by these pests was almost the same as in the control variant (Table 3). Reduction of the absolute cone damage (D_a) by both the pests ended in a failure. Thus, the level of seed damage was approximately the same as in the control variant.

Cimbush failed to reduce cone damage by the remaining insect species either. Nevertheless, injections of the insecticide influenced to some degree the populations of C. strobilella (L.) and K. strobi (Winn). Thus, the absolute cone damage (D_a) by C. strobilella (L.) was reduced from averagely 0,6 specimens per cone in the control variant to 0,5 spec./cone after cimbush application, while the absolute damage (D_a) by K. strobi (Winn.) was reduced from 0,7 spec./cone to 0,6 spec./cone, respectively (Table 3).

In the treatment the summarized seed loss due to insects averaged 32% (Table 2). As compared with the standard (BI-58) seed damage here increased by 120% with the significance of difference being $p>0,05$, while in comparison

Table 4. Effects of insecticide-injections to seed damage by conobiont-phytophagan populations

Treatment	Mean number of seeds damaged by conobiont-phytophagan populations (L), %								Total
	Dioryctria schuetzeella	*Ernobius tabidus*	*Cydia strobilella*	*Dioryctria abietella*	*Eupithecia* sp.	*Kaltenbachiola strobi*	*Lasiomma anthracinum*	*Megastigmus abietis* - *Plemeliella abietina*	
Antio, 25% e.c.	2,1	0,1	5,7	8,6	1,3	0,4	3,9	1,7	23,8
Cimbush, 25% e.c.	0,3	1,9	6,5	11,4	3,3	0,6	6,1	1,6	31,7
BI-58, 40% e.c. (standard)	-	-	4,-	4,5	1,2	0,4	2,3	2,0	14,4
Control	1,8	1,6	8,2	11,7	3,2	0,6	9,8	4,4	41,3

Table 5. Effects of trunk-injected insecticides on seed damage by seminiphagous insects (Megastigmus abietis and Plemeliella abietina)

Treatment	Number of seeds analysed	Mean number of damaged seeds, %		
		Megastigmus abietis	Plemeliella abietina	Total
Antio, 25% e.c.	2500	1,-±0,2	0,7±0,1	1,7±0,3
Cimbush, 25% e.c.	2500	1,1±0,2	0,5±0,1	1,6±0,2
BI-58, 40% e.c. (standard)	2500	1,9±0,1	0,1±0,0	2,-±0,1
Control	2500	3,1±0,3	1,3±0,3	4,4±0,5

with the control it decreased by 23%. In the treatment with cimbush the total seed loss due to M. abietis (Seitn.) and P. abietina (Seitn.) was on an average 1,6 - 0,2%, i.e. almost the same as after antio application (Table 5). As compared with the control, damage done by both the species was reduced by more than 2,5 times.

CONCLUSION

On the whole the experiments have shown that the systemic insecticide BI-58, 40% e.c. was the most effective for seed crop protection of Norway spruce (Picea abies Karst.). After this treatment young female buds were completely safe from pest damage. Cone and seed damage by insects here was reduced by 2 and 2,8 times respectively (Table 2), while the absolute number of all insects in cones (D_a) - by 2,6 times (Table 3). The absolute cone damage by L. anthracinum (Czerny.) and D. abietella (Den. et Schiff.) was reduced by 3 and 4 times (Table 3), while seed loss - by almost 77 and 62% respectively (Table 4). Besides, treatments showed that seed damage by the larvae by P. abietina Seitn. was significantly reduced after the insecticides' application (Table 5).

Injections of the systemic-contact insecticide antio, 25% e.c. were less effective. As compared with the previous treatment, the absolute cone damage (D_a) by insects increased by 50% (Table 3), while seed losses by 65% (Table 2). However, antio was more effective than cimbush in protecting cones and seeds by 21 and 25% respectively. The best results antio gave as applied against L. anthracinum (Czerny.). In comparison with the control seed damage by the pest decreased by 60% (Table 4).

Among the tested insecticides cimbush (25% e.c.) was significantly less effective. Only 11% of cones were protected in this treatment with the significance of variance in comparison with the control being $p<0,05$ (Table 2). To the injections of this insecticide reacted mostly L. anthracinum (Czerny.) and C. strobilella (L.). Mean number of cones damaged by these pests was reduced by 30 and 14% (Table 3), while seed loss - approximately by 38 and 21% respectively (Table 4). After the application of cimbush seed losses due to seminiphagous insects (M. abietis Seitn. and P. abietina Seitn. was reduced by 2,7 times (Table 5), while the damage of female buds - by 1,5 times (Table 3).

In the course of the whole vegetative season the toxicity of insecticides to trees was not detected. Seed germination in all experimental trials corresponded to the standard requirements for the first class seeds (85,7-87%) of Norway spruce (Picea abies Karst.). Thus, to make cone and seed protection more effective the dose of BI-58 at 0,5 g/cm (or 0,2 g/cm a.i.) may be greater in subsequent trials. According to some authors the larvae of L. anthracinum (Czerny.) and the caterpillars of C. strobilella (L.) are completely killed after the application of commercial formulations of phosphamide (BI-58) at the rate of 1 g/cm stem diameter (or 0,4 g/cm a.i.) at the height of 10-12 m (Stadnitskiy et al., 1978). Besides, it was noted that phytotoxicity of the preparation to spruce is not obvious even at the rate of 5 g (or 2 g/cm a.i.) per 1 cm of trunk diameter (Smetanin, 1977).

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LITERATURE CITED

Dumcius, O., 1985: Norway spruce (Picea abies Karst.) seed yield protection by crown treatment with sulfitic alkali (in Russian). Proceed of sc. works: Plant protection in the pre-Baltic republics and Byelorussia. Part II. Tallin, 115-116.

Dumcius, O., 1986: Tests of pine needle acetone extractions for Norway spruce (Picea abies Karst.) seed yield protection against insects (in Russian). Proceed. of sc. works: Integrated forest protection against pests and diseases. Section I, Kaunas, 22-23.

Filer, T.H.: 1973. Pressure apparatus for injecting chemicals into trees. Plant Dis. Report. 57, N 4.

Fogal, W.H., and S.M. Lopushanski: 1983. Stem injections of insecticides for control of white spruce seed and cone insects. Proceed. of the 1st conference of cone and seed insects W.P. IUFRO S2.07.01. Athens, Georgia, USA, 157-168.

Helburg, L.B., M.E. Schomaker and R.A. Morrow, 1973: A new trunk injection. Plant Dis. Report, 57, N 6.

Koerber, T.W., and G.P. Markin, 1983: Metasystox-R injections increase seed yield of Douglas-fir in California, Oregon and Washington. Proceed. of the 1st conference of cone and seed insects W.P. IUFRO S2.07-01. Athens, Georgia, USA, 137-147.

Merkel, E.P., 1970: Trunk-implanted systemic insecticides for slash pine cone insect control. Fla. Entomol. 53, N 3. 143-146.

Merkel, E.P., and G.L. De Barr, 1971: Trunk implantations of dicrotophos for cone-insect control in slash pine seed production stands. J. Econ. Entom. 64, N 5.

Naumov, F.V., A.M. Bortnik and G.V. Stadnitskii. 1976. Protection of forest objects from insects by implantation and lubrication of chemicals (in Russian). Proceed. of sc. works: The main trends of investigations in the sphere of chemical means for plant protection and weed control. Moscow. 138-139.

Reardon, R.C., L.E. Stipe and J.E. Dewey. 1983. Implantation and injection of systemics for seed yield increase of Douglas-fir in Montana. Proceed. of the 1st conference of cone and seed insects W.P. IUFRO S2.07.01. Athens, Georgia, USA, 187-193.

Reardon, R.C., L.J. Barrett, T.W. Koerber, L.E. Stipe and J.E. Devey, 1985: Implantation and injection of systemics to suppress seed and cone insects in Douglas-fir in Montana. Can. Entom. 117, N 8, 961-969.

Smetanin, A.N. 1976: Wood plant protection by pesticide injections (in Russian). Bull. of the Main. Bot. Garden. Moscow, issue 99, 111-113.

Smetanin, A.N., 1977: Seed protection of coniferous species in forest-reserves (in Russian). Kiev, 59 p.

Stadnitskii, G.V., V.P. Grebenshchikova, F.V. Naumov, and A.M. Bortnik, 1978: Protection of reproductive organs of coniferous species in seed sites and plantations (in Russian). Leningrad. 66 p.

Stadnitskii, G.V., G.I. Iurchenko, A.N. Smetanin, V.P. Grebenshchikova and M.V. Pribylova, 1978: Conifer cone and seed pests (in Russian). Moscow, 168 p.

Summers, D., and G. Miller, 1986: Experience with systemic insecticides for control of cone and seed insects in Douglas-fir seed orchards in coastal British Columbia. Proceed of the 2nd conference of cone and seed insects W.P. IUFRO S2.07-01. Briancon, France. 267-283.

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